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THE UNIVERSITY OF ALBERTA

THE DENTAL MORPHOLOGY
OF THE
SOUTHERN ONTARIO IROQUOIS

BY

Ⓒ G. STEWART TAIT

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF ARTS

DEPARTMENT OF ANTHROPOLOGY

EDMONTON, ALBERTA
SPRING, 1988

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled THE DENTAL MORPHOLOGY OF THE SOUTHERN ONTARIO IROQUOIS submitted by Gary Stewart Tait in partial fulfilment of the requirements for the degree of Masters of Arts.

....
(Supervisor)

....

L. M. Fedigan

Mary Jackes

Date: 27th April 1988

ABSTRACT

This thesis has three main objectives:

(1) to describe the skeletal Iroquois population from the Grimsby site using different dental traits believed to have some discriminatory value in odontological studies;

(2) to use the frequencies of the most reliable of these traits in a biological distance analysis of several Iroquoian groups from southern Ontario, including the Grimsby population; and

(3) to formulate general conclusions regarding the utility of dental features for biological comparisons of this kind.

The main focus of the thesis was a morphological examination of the teeth of the Neutral Iroquois population which occupied the Grimsby site around AD 1620-1650. The study sample consisted of a series of dental impressions; these included casts of 67 maxillae and 66 mandibles, representing 63 adults and seven juveniles. The mature individuals had been sexed in a previous osteological study of the Grimsby remains.

The Grewal-Smith Mean Measure of Divergence was the formula employed for the relative distance comparisons of five skeletal samples from southern Ontario. Three of these samples were Neutral groups (viz. Grimsby, Carton and Shaver Hill), while the other two were possibly Huron populations

(viz. Kleinburg and Sopher). The analysis demonstrated that the Carton and Shaver Hill populations were the two most closely related groups, while the Grimsby and Kleinburg populations were the most distantly related; the last was the most distinct of the five dental samples. The position of the Sopher population was ambiguous; its apparent affinity with the Carton-Shaver Hill group-cluster was probably the result of several factors, including gene flow with the latter, as well as interobserver scoring error.

The significance of interobserver error is always a major concern in a biological distance analysis, such as the one presented here, which uses samples scored by different workers. An intergroup comparison of theta values, on a trait by trait basis, revealed that some dental features were less prone to this problem than others. Overall, the analysis of theta values indicated that the MMD results of this investigation cannot be explained simply by interobserver scoring variance or by geographic proximity of the study populations.

ACKNOWLEDGEMENTS

I would like to thank the members of my thesis committee for their participation in the process of thesis revision and defense. I am grateful to Dr. L.M. Fedigan for her willingness to venture into the strange and alien world of dental morphology. I am very appreciative of the comments and guidance given by Dr. O.B. Beattie, who consented to act as my thesis advisor, and also for his patience in regard to the completion of this work, which at times seemed likely to drag on to the "crack of doom". A great debt is owed, as well, to Dr. G.H. Sperber, for the time he spent on several occasions describing and rating diagnostic dental features in a number of casts.

My deepest gratitude goes to Dr. M.K. Jackes, who secured the Grimsby cast material for my study and who provided the statistical programs necessary for the determination of sexual dimorphism in dental trait expression, and biological distance estimations for several Iroquoian groups. Her assistance in these computations and in their interpretation was invaluable. Also, the previous work she completed on the Grimsby skeletal material allowed the assignment of sexual identity to most of the dentitions examined.

Finally, I must express my appreciation to a number of individuals who made translations of several German articles for my benefit, namely: Mrs. Erika Ewen, Miss Anja Zeidler and Dr. W.M. Schultz.

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CHAPTER 1.

INTRODUCTION TO IROQUOIAN STUDIES AT GRIMSBY AND OTHER SITES.

1.1 Background to Grimsby Site.

The Grimsby site is located near the southwestern shore of Lake Ontario, about halfway between the cities of Hamilton and St. Catharines, Ontario. The locale is in the heart of what was formerly the territory of the Neutral Iroquois (Noble, 1978). The excavation was carried out between mid-October, 1976 and early April, 1977, under the direction of W.A. Kenyon, of the Royal Ontario Museum (Kenyon, 1982:5,8). The cultural and human remains were originally dated to AD 1640-1650, on the basis of historical manuscripts and the large quantity of trade goods found with the burials (Kenyon, 1982:226; Jackes, 1983). According to Kenyon and Fox (1982), a better estimate for the Grimsby site span would be AD 1615-1650. This period would represent the last few decades of the Neutral, as the confederacy was destroyed and its people scattered by the Five Nations Iroquois between 1650 and 1653 (Hunt, 1940:97-98).

The Grimsby project was a salvage operation, and it was hampered by a number of legal and technical problems (Kenyon, 1982: 5-8; Jackes, 1983; Jackes, in press). The locale had been superficially disturbed by relic-hunters before the ROM crew began to work, and during late December some of the unearthed materials were disarranged by vandals during a suspension of digging activity. A major difficulty was that human bones could not be cleaned or marked, so that the checking of individual specimens was not possible, and cataloguing accuracy was reduced. Anomalous or doubtful features could not be studied intensively at a later date, because all the skeletal material had to reburied by the summer of 1977.

However, the digging was done in an orderly fashion, the skeletal remains were photographed before removal, X-rays were taken of some specimens and the notes of excavators provided additional data (Kenyon, 1982: 5-8; Jackes, 1983). There was enough information to indicate that the burial patterns at Grimsby more closely resembled those of the Erie and Seneca than those of the Huron, contrary to what had previously been assumed (Kenyon, 1982: 228-229; Jackes, in press). The American Iroquois were inclined toward cemetery-type graves, where the continued association of parts from the same body was desirable, while the Huron custom of ossuary sepultures ensured that bones from different individuals would be inextricably mixed together.

A careful and detailed statistical and morphological analysis by M.K. Jackes resulted in the identification of 373 individuals at the Grimsby site, from a total of 58 different burial-features (Kenyon, 1982:230; Jackes, in press). Of these features, there were three (Fe6, Fe7, Fe37), representing seven individuals, which were really just clusters of disturbed bone. However, there were also 26 single interments, 17 small (family?) group-sepultures of two to four persons, and two rather large graveyards (Fe9 and Fe62), containing 58 and 103 bodies. The remaining 10 features each held from 5 - 25 individuals (Jackes, in press).

According to Kenyon (1982:231), four types of graves were encountered: (1) the primary or "simple flex" burial, (2) the "true" bundle-burial; (3) the "scattered" bundle-burial (characteristic of Huron ossuaries) and (4) the semi-articulated bundle-burial. There were an estimated 50 (more or less) articulated skeletons which represented about 14% of the MNI total; the remainder had been disarticulated to some significant degree before interment. The carefully ordered, multi-individual bundle-burial pattern observed at Grimsby has also been noted for other Neutral sites, e.g. Shaver Hill and Walker (Jackes, in press).

Jackes (1983; 1986) has provided a detailed study of the demographics of the Grimsby people. Of the 373 recovered individuals, 28.5% were mature males and 27.2% were mature females, while 2% were indeterminable adults and 42.7% were juveniles under 20 years of age (35 being over the age of 15 could be sexed). The population represented by the Grimsby remains probably numbered between 200 and 300 individuals at any one time.

1.2 Grimsby dental material.

The teeth of the Grimsby population were initially studied by Peter Hall, during the winter of 1976-1977 (Jackes, in press). Hall coded data on wear and pathology for later statistical analysis, and also provided miscellaneous observations on specimens and casts in his notebook on the Grimsby material. M.K. Jackes (in press) completed the analysis and wrote up the results and conclusions in her manuscript on the skeletal remains.

Through the efforts of Jackes, a series of dental casts was made of some of the gnathic specimens, before these had to be reburied. The cast sample provided the study material for this thesis, and included 67 maxillae and 66 mandibles, representing 63 adults (permanent dentitions) and seven juveniles (mixed dentitions). In addition to the above, there were also eight plaster impressions made of the upper and lower jaws of four infants under the age of five. The deciduous teeth were considered in a separate manuscript.

1.3 A brief history of Iroquoian peoples (AD 1600-1700).

The Grimsby Neutral population belonged to the Iroquoian stock, most of which inhabited or eventually settled in the Lower Great Lakes region of southeastern

Ontario and northern New York (see Figure 1, pp. 6-7). At the time of European contact, ca. AD 1600, the aboriginal peoples of this region were organized into three major confederacies, the Huron (five tribes), the Neutral (five or six tribes) and the famous League of the Five Nations, as well as a number of much smaller (tribal?) groups, viz. the Petun or Tobacco-Huron, the Erie, the Wenro, and the St. Lawrence Iroquois (Heidenreich, 1971:81-86; White, 1972; Spencer et al., 1977:367-368). These smaller entities were at times allied or associated with one or the other of the different confederacies (Ibid.; Hunt, 1940:50,101).

The pre-contact Great Lake Iroquois are believed to have inhabited the area for at least a couple of millenia (Spencer et al., 1977:373-378; see Figure #2, p. 8). Two other affiliated tribes, the Susquehanna and Conestoga, originally occupied parts of eastern Pennsylvania (Hunt, 1940:137), but moved north in the mid-seventeenth century into the adjacent areas of New York. A third group, the Tuscarora, migrated from the Carolinas and had joined the League by 1715, leaving the south Appalachian Cherokee Confederacy as the only major Iroquoian division existing outside the Great Lakes-Empire State region (Spencer et al., 1977:367-368).

The Iroquoian cantons of the League are the only groups to survive as distinct entities, having dispersed or destroyed the other northern confederacies and tribes, some

Figure 1. Map of northern Iroquois (c. 1600) and sites cited in text. (Key and References).

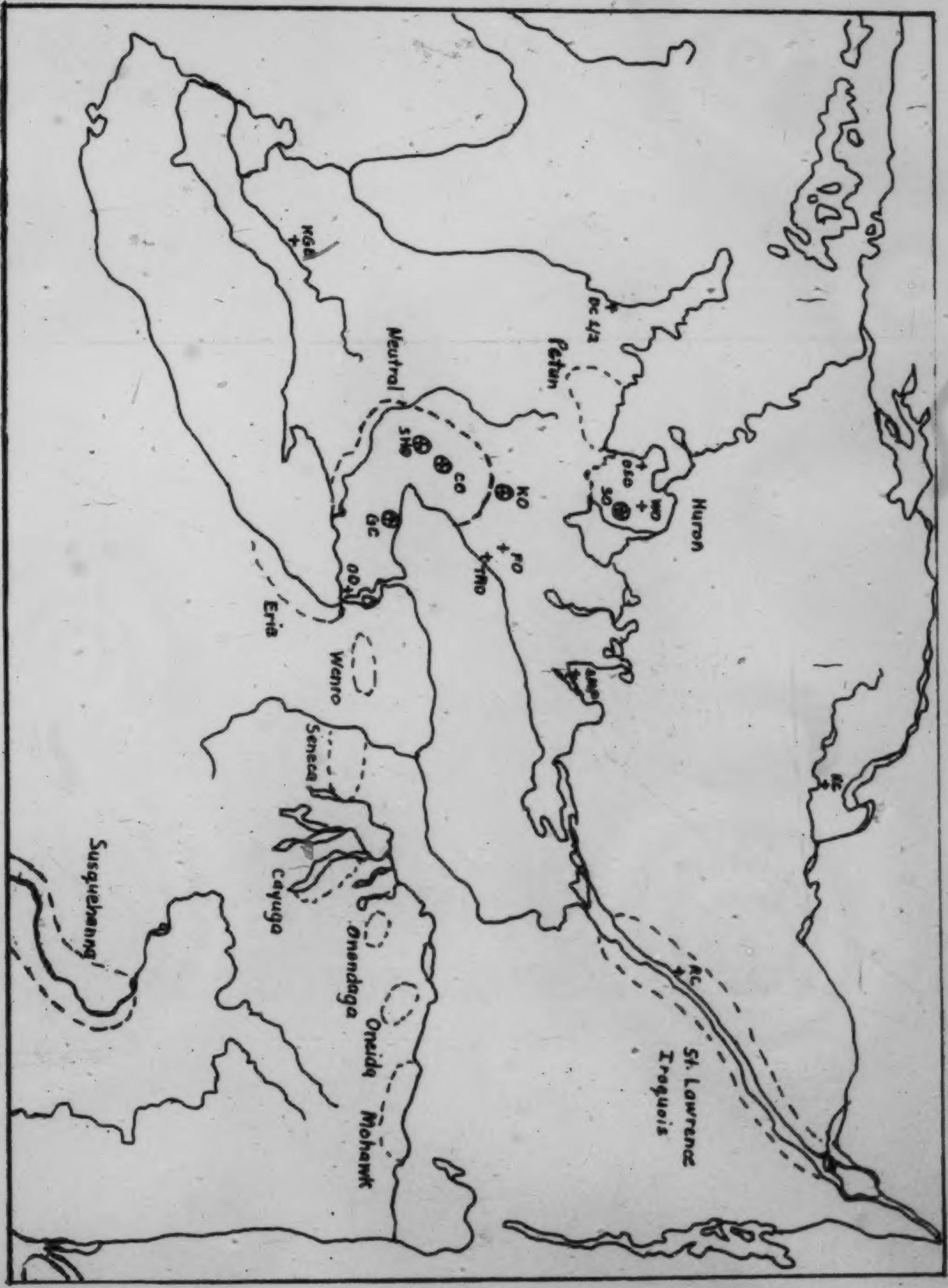

KGd
DC 4/2
Petun
Neutral
SHO
CO
KO
BC
OO
Erie
Wenro
PO
MO
OSO
SO
WO
Huron
AWE
Seneca
Cayuga
Onondaga
Oneida
Mohawk
Susquehannock
RC
RC
St. Lawrence
Iroquois

Figure 1. Map of northern Iroquois (c. 1600) and sites cited in text: Key and References.

Key (* = Site populations used in MMD analysis.)
St. Lawrence Iroquois
RC = Roebuck Cemetery (AD 1450-1530)

Early E. Ontario Iroquois/Proto-Iroquois
KC = Kant Cemetery (?AD 0-200)
SMP = Serpent Mounds/Cemeteries (AD 0-300) & Pits (AD 800-1200)

Early W. Ontario Iroquois/Proto-Iroquois
DC 1/2 = Donaldson Cemetery 1 (630-470 BC) and Cemetery 2 (70 BC - AD 80)

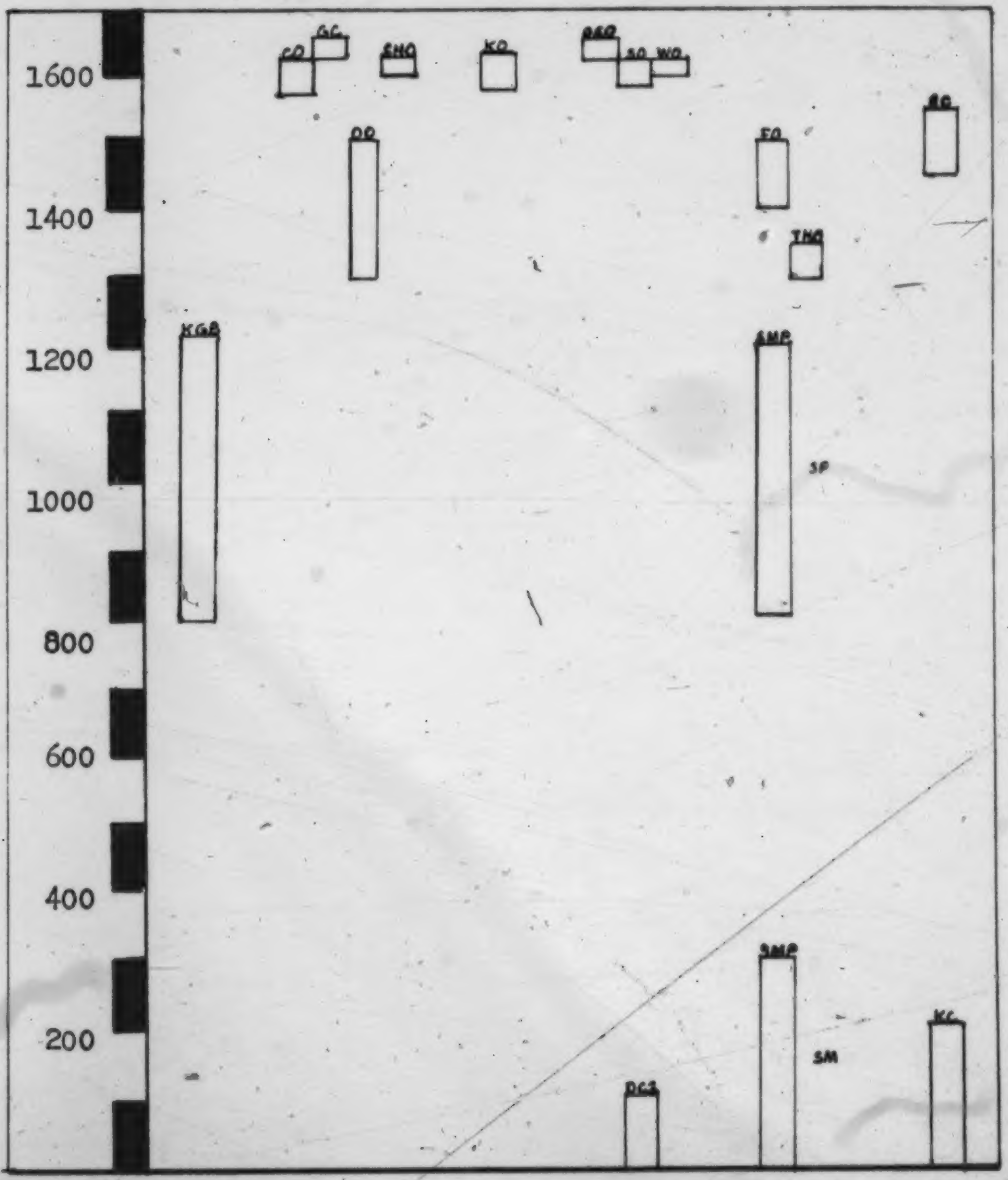
Proto-Huron (?) Iroquois
FO = Fairty Ossuary (AD 1400-1500)
THO = Tabor Hill Ossuaries (AD 1300-1350)

Huron Iroquois
*KO = Kleinburg Ossuary (AD 1585-1615) - N.B. May be a Neutral population
OSO = Ossossane Ossuary (AD 1624-1636)
*SO = Sopher Ossuaries (AD 1580-1610)
WO = Warminster (Cahiaqúe) Ossuary (AD 1600-1630)

Neutral Iroquois
*CO = Carton Ossuary (AD 1580-1610)
*GC = Grimsby Cemetery (AD 1620-1650)
OO = Orchid Ossuary (AD 1300-1500)
*SHO = Shaver Hill Ossuaries (AD 1600-1620)

Adapted from:
(1) Wright, 1974:47, Map 1.
(2) Kenyon, 1982:229, Figure 143.
(3) Molto, 1983:37, Figure 2.1.
(4) Molto, 1983:87-88, Figure 2.2, Table 2.1.
(5) Patterson, 1984:8-9, Figure 2.1.

Figure 2. Chronology of aboriginal cultures of southern Ontario (AD 0 - 1700).



Adapted from:

Wright, 1974: 61,63,66; Molto, 1983: 88, Table 2.1; Patterson, 1984: 11-15, Figure 2.2, Table 2.1.

of which were weakened by introduced diseases, before the end of the seventeenth century (Hunt, 1940:87-104). The Great Lakes Iroquois, including the Neutral, were utterly routed and scattered (or absorbed) within a single decade (1645-1655). Therefore, their history and ethnology can only be partially reconstructed, by archaeological work and analysis of pre-contact and post-contact sites, and by the interpretation of contemporary European accounts.

1.4 A brief history of Iroquoian dental studies.

The first worker to investigate Iroquoian skeletal biology was Sir Daniel Wilson (1857, 1862, 1873), who was primarily concerned with the craniometry of the "Huron race" and said little about the dentition. More than six decades passed before the next publication of importance, this being Sir Francis Knowles' (1937) study of the Roebuck site material. Knowles considered metrical and nonmetrical, cranial and postcranial variation, and provided demographic information. He also presented data on dental pathology from five sites in southern Ontario, including Roebuck, and noted the occurrence of agenesis and dental anomalies (e.g. supernumerary teeth) in some specimens (Knowles, 1937:5-6, 12-13,48-49,70-75).

Subsequent research into Iroquoian dentitions dealt mainly with the pathology (caries, abscessing, periodontal disease, malocclusion) of human remains, e.g. from Huron ossuaries at Warminster (Harris, 1949) and Ossossane (Gruber, 1958). Some papers also included a few remarks on attrition, but very little was said about tooth morphology, e.g. in the skeletal populations at Kant (Emerson, 1956; Popham, 1956) and Krieger (Kidd, 1956). The only other publication of note during this period (1850-1960) dealt with the demography of the Tabor Hill ossuary (Churcher and Kenyon, 1960).

During the next decade, J.E. Anderson founded the basis for future work in the field of aboriginal skeletal biology in southern Ontario. From 1961 to 1969, he completed several important investigations on the remains of Ontario Iroquois, e.g. at the Fairty and Serpent Mounds sites. His major papers (1964; 1968) provided the organizational scheme followed in the reports and theses of his students at the University of Toronto (Cybulski, 1968; Melbye, 1969; Ossenberg, 1969; Webb, 1969).

Anderson established a problem-oriented approach, linked to archaeological theory and research. This emphasized nonmetrical data in the examination of intrademic and interdemic variation, rather than the craniometry and osteometry which had previously dominated skeletal studies. Anderson (1968) and his students (Ossenberg, 1969; Webb, 1969) also introduced the first crude statistical techniques (Chi-Square, Penrose Size and Shape, Clark's Coefficient of Divergence) into their assessment of population affinities, using a battery of morphological traits in the analysis.

Anderson (1964) and his associates (Cybulski, 1968; Melbye, 1969:76-79; Ossenberg, 1969; Webb, 1969:77-80) provided more detailed descriptions of Iroquoian teeth in their reports on site remains. The main focus of these descriptions was on pathology and attrition (Anderson, 1968; 1969a), but there was also a presentation of statistics on several basic morphological traits, e.g. shovel-shaping of the incisors, upper molar cusp-number, lower molar cusp and groove patterns, accessory cusps (Carabelli and paramolar tubercles) and molar-crown enamel extensions. Observations on dental agenesis and dental anomalies (e.g. supernumerary and peg elements) were also given by these workers.

In the last 15 years, there has been a trend toward specialization in thesis research, and the use of more refined and powerful multivariate statistical techniques. A number of graduate students have con-centrated on particular aspects of Iroquoian skeletal biology, e.g. the Huron spine (Jackes, 1977); dental and osteal pathology (Hartney, 1978); discontinuous cranial morphology (Molto, 1983); and dental pathology and attrition (Patterson, 1984). Others have continued to write on "site" populations and include a section on tooth pathology and morphology (Jerkic, 1975; Pfeiffer, 1976; Kolar, 1982).

It has only been recently that intensive research has been done on Iroquoian tooth morphology. Sirianni (1967) and Winnicki (1969) had written short manuscripts on the Orchid and Carton dentitions, but the pioneering work in this area was P.J. Wright's (1974) M.A. Thesis. Wright examined a number of discrete and quasicontinuous dental traits in order to describe the dental morphology of three Iroquoian skeletal populations (Carton, Shaver Hill and Sopher) and assess their relationships by using Chi-Square (X^2) analysis.

The latest investigations into Iroquoian dental morphology were carried out by K.E. Wright (1977), in her M.A. Thesis on the Kleinburg teeth, and J.E. Molto (1979), in his study of the Donaldson material. The former used P.J. Wright's (1974) work as a basis for her own research, and followed most of his standards, in order to make their observations comparable. She then used biological distance formulae, viz. Grewal-Smith's Mean Measure of Divergence (MMD) and Sanghvi's G-statistic, to assess the interdemic relationships of four sites: Carton, Shaver Hill, Sopher and Kleinburg. Molto examined the dentitions of the Donaldson populations as part of his comparison of these groups with samples from other southern Ontario sites.

1.5 Sexing of Grimsby dentitions.

The skeletal remains at Grimsby were sexed by M.K. Jackes (in press). Most of the dentaries studied in this thesis were associated with pelvic or cranial elements; 30 individuals (18 males, 12 females) were sexed on the basis of pelvic traits and 26 (10 males, 16 females) on the basis of cranial morphology and metrical analysis. It should be noted that an accuracy of 90% - 95% can be attained using pelvic features (Brothwell, 1972:54) and possibly of 90% using cranial characters (Anderson, 1969b:160). There were 11 indeterminable skeletons; these included both juveniles and adults.

The three remaining specimens consisted of two isolated (male?) upper and lower jaws (Fe36#6003 and Fe36#7001, respectively), and a gnathic set that very probably belonged to (but was not definitely associated with) a female cranium (Fe62#63). The maxillae and mandible of Feature 36 are very likely to be male elements, according to Jackes (pers. comm., 30/5/85). However, in the tables presented in each tooth-class chapter, figures which include the doubtful male and female dentitions will be underlined (for the descriptive categories affected).

CHAPTER 2.

THEORETICAL BACKGROUND AND METHODOLOGY.

2.1 Introduction.

In this chapter, the general rationale for dental studies in the context of physical anthropology is given, and the method used in the pursuit of the objectives outlined below. A short section dealing with the nomenclature employed in the text is also included, so that the basic terms are clearly understood.

The general objectives of this thesis are the following:

(1) to describe the variations of different traits that are believed to have discriminatory value in dental population studies;

(2) to use the frequencies of the most reliable of these traits in a biological distance analysis of several Iroquoian populations; specifically, those represented at the archaeological sites of Grimsby, Shaver Hill, Carton, Kleinburg and Sopher.

(3) to draw some general conclusions in regard to the utility of dental morphological traits for biological distance analysis, and the relative utility of different anatomical features.

2.2 Theoretical background to dental studies.

The dental trait battery is perhaps the most useful tool for studying biological relationships between skeletal populations, and is also of value in analyzing intergroup differences among living peoples. This belief is based on three main factors:

(1) no skeletal units of similar size can yield so much morphological information; there are numerous apparently discrete traits present on each tooth, particularly in the case of premolars and molars (Kraus et al., 1969:293; Taylor, 1978:353);

(2) phenotype expression of many features seems to be largely determined by genetic factors (Kraus et al., 1969:293-296);

(3) the tremendous durability of the teeth; at many archaeological sites, dental elements are the only skeletal parts found in any abundance or preserved well enough for analysis, e.g. in the Sopher ossuary, where the constituent bones were very badly damaged by heavy water saturation of the surrounding earth (Wright, 1974:66,206).

It should also be noted that dental casts can be taken of living individuals, so that large samples drawn from extant populations can be studied (Scott and Dahlberg, 1982; Scott et al., 1983); this is very difficult to do (without radiographs) for most cranial and postcranial discontinuous traits. This factor has enabled some researchers to study the changes in gene or character frequencies that have occurred through time in some microgeographic populations, e.g. East Greenland Eskimos (Pedersen, 1949) and Aleuts (Turner, 1967b).

The transmission of dental characters was originally studied in the nineteenth century, by means of genealogical data, and the features considered were those of a conspicuous and abnormal nature, such as hypodontia, hyperdontia and peglike or conoid elements (e.g. McQuillen, 1870; Cope, 1886a). With the rediscovery of Mendel's Laws in the early twentieth century, the analysis of family histories became an important and widespread method of determining the inheritance of dental anomalies, particularly missing and conoid upper incisors. Two opposing unifactorial models based on pedigree information were commonly used to account for the associated agenesis and peg-tooth phenotypes: an autosomal recessive-allele hypothesis and an autosomal dominant-allele hypothesis (Thomas, 1926; Keeler, 1935; Dahlberg, 1937; Montagu, 1940; Iltis, 1948; Thomsen, 1952; Grahnén, 1956; 1957; Alvesalo and Portin, 1969; Woolf, 1971).

However, studies involving statistical analysis of the occurrence of missing elements from different parts of the dental arcade indicated that the inheritance of hypodontia was much more complex than previously thought. Several investigations have established a highly-significant correlation between the incidence for absence and reduction of specific anterior and posterior teeth and that for multiple agenesis (e.g. Brekhus, Oliver and Montelius, 1944; Grahnén, 1956; 1957; Garn et al., 1963; Le Bot and Salmon, 1977). Grahnén (1956, 1957) also demonstrated that there was a significantly higher frequency of missing incisors and premolars in the parents and siblings of propositi with hypodontia than in the general population. Similar results have been obtained by other researchers (Garn et al., 1963; Le Bot and Salmon, 1977).

The realization that hypodontia has a rather involute and manifold nature has led to the gradual acceptance of more complex models of inheritance. A number of workers have noted that a polygenic hypothesis could account for their results as well as a monogenic one (e.g. Grahnén, 1956; 1957; Alvesalo and Portin, 1969; Woolf, 1971). Witkop (1961) suggested that two separate loci are involved in incisor reduction and absence: one controlling timing of tooth-development and the other degree of tooth-suppression. Chung et al. (1972) supported a multifactorial mode of transmission and a quasicontinuous mode of expression for missing and peg-shaped incisors. Suarez and Spence (1974) demonstrated that a simple Mendelian model could not fit their pedigree data for agenesis, while a multigenic, multithreshold model could not be rejected.

The evidence for inheritance of hyperdontia is not as substantial as that for hypodontia. Some workers have suggested that a single autosomal dominant or recessive locus might be responsible for certain cases of additional teeth (e.g. Keeler, 1935; Niswander and Sujaku, 1963). Recently, evidence from family-history and identical-twin studies has supported the idea that accessory elements are heritable to some degree (Mercuri and O'Neill, 1980; Rubin et al., 1981; Zvolanek, 1981). Several investigations have demonstrated statistically-significant associations of hyperdontia with males and hypodontia (or conoid incisors) with females (e.g. Niswander and Sujaku, 1963; Davies, 1968c; Chung et al., 1972; Brook, 1984). Brook (1984) has concluded that supernumerary teeth and missing teeth are probably manifestations of the same polygenic and multithreshold developmental complex.

Gross genetic abnormalities are in some instances related to dental anomalies as well as to less striking variations of the tooth crown. Nasjleti et al. (1966) found an extra chromosome 22 (forming a trisomic mutant) associated with a case of unilateral premolar genesis. Several unusual dental characters are commonly observed in individuals suffering from Down's syndrome (trisomy of chromosome 21); these include shovel-shape form of the upper incisors, reduced or missing hypocone in the first and second upper molars, and occasionally, peglike anterior elements (Cohen et al., 1970). Males with a supernumerary Y-chromosome (trisomy XYY) manifest a significantly stronger expression of the shovel-shape feature in the upper lateral incisor than do normal relatives (Kirveskari and Alvesalo, 1981). In Turner's syndrome (monosomy for chromosome X), the affected females show a significantly weaker expression of the shovel-shape phenotype in the upper lateral incisor and a significantly greater reduction of the hypocone in the first and second upper molars than do normal relatives (Kirveskari and Alvesalo, 1982).

The association of specific crown traits with genetic factors goes back to the work of Black (1890:61; 1897:63), who stated that the Carabelli pit/tubercle complex was an hereditary feature. Hrdlička (1908) thought that the barrel-shaped incisor sometimes found in Amerindians was transmitted as a racial "specialization". His later work (Hrdlička, 1911; 1920) on the shovel-shaped incisor convinced him that this particular character was of a racial and phylogenetic nature. Hellman (1928) came to a similar conclusion regarding the cusp and groove patterns found on the lower molars of modern man.

However, the first major investigation into the inheritance of crown traits was made by Korkhaus (1930). He examined the degree of concordance of several dental characters for each set of 48 monozygotic (identical) twin pairs and 33 dizygotic (fraternal) twin pairs. These characters included shovel-shaped incisors, the Carabelli complex and occlusal surface patterns of the lower molars. Korkhaus found that almost every crown feature was concordant for the monozygotic twin pairs, but this was not the case for the dizygotic twin pairs. These results suggested that the features studied were to some degree genetically-controlled attributes.

Other research has also indicated that identical twins manifest greater intrapair concordance for dental variations than fraternal twins. Euler and Ritter (1940) showed this was the case for the form and size of the Carabelli polymorphism. Kraus (1957) found a highly significant difference between monozygotic twins and dizygotic twins in intrapair concordance for 16 lower first premolar traits. The disparity between identical-twin concordance and nonrelated-pair concordance was also determined to be highly significant. A comparable investigation by Ludwig (1957) using seven lower second premolar characters yielded similar results. A significant difference in intrapair concordance between monozygotic twins and dizygotic twins ahs been demonstrated for as many as 45 molar features, including the Carabelli complex, cusp number and various groove and stria patterns (Zoubov and Nikityuk, 1978).

Research by several workers on the determination of twin and triplet zygosity has demonstrated that the results obtained from intraset concordance analysis using dental characters are in strong agreement with those based on serology. Lundstrom (1963) was able to diagnose identical twins with an accuracy of 90% - 95%, using a combination of several features, e.g. facial-ridging of the anterior teeth, molar cups-number, groove-pattern, and crown-shape. Wood and Green (1969) identified monozygotic twins with an accuracy of almost 90% by employing Ludwig's premolar variations in their dental battery. Kraus, Wise and Frei (1959) found that their classification of a small group of triplets into monovular, diovular or triovular categories by means of an array of premolar traits was in complete agreement with the blood-typing analysis.

Kraus (1951) made the first systematic pedigree analysis of a regular crown feature, the Carabelli complex, in several Mexican and Papago families. He found that his results could be explained by the hypothesis of a single automosal gene with two codominant alleles. Tsuji (1958) undertook a similar investigation of the same polymorphism in 28 Japanese families and concluded that trait presence was determined by a single dominant allele with incomplete penetrance. An Amerindian lineage study by Dahlberg et al. (1956) supported the idea that a multi-allele, unifactorial system controlled the shovel-shape expression. Menegaz-Bock and Dahlberg (1960) demonstrated the occurrence of highly significant interfamilial variation compared to intrafamilial variation, in the fossa depth of the shovel-shaped incisors of Pima propositi. Other research using Amerindian pedigree data indicated that a Mendelian dominant gene model with incomplete penetrance was probably responsible for observed protostylid phenotypes (Dahlberg and Fukuhara, 1964).

Portin and Alvesalo (1974) completed a major genealogical study on the transmission of the shovel-shape feature on the upper central incisor in a Finnish sample from Hailuoto Island. They determined that siblings of affected propositi showed a significantly higher incidence of the trait than siblings chosen at random from the general sample. Pedigree and population data supported an inheritance model of one autosomal locus with two codominant alleles, but also fitted a multifactorial or milti-allele, unifactorial model.

Recent investigations using lineage and family history analysis have strongly suggested that dental traits are multifactorial and quasicontinuous in nature (e.g. Sofaer et al., 1972a; Scott, 1973:109-113; 1974; Baume, 1975; Blanco and Chakraborty, 1976; Smith, 1977; Berry, 1978; Harris and Bailit, 1980; Kolakowski et al., 1980; Dahlberg et al., 1982). In general, these studies ahve indicated a relatively high and significant degree of heritability for some crown features but not others. According to Blanco and Chakraborty (1976), almost 70% of the total variability observed in upper central incisor shovel-shape can be attributed to the additive effect of several loci. Harris and Bailit (1980) estimated the additive genetic component for distal fifth-cusp expression to be about 65% on the upper first molar.

Complex, multifactorial models of trait inheritance have only recently become popular among dental anthropologists. In the four decades following Korkhaus' seminal study, most adontologists proposed simple Mendelian-gene hypothese to account for the phenotypic variation seen in such features as the Carabelli complex, the shovel-shape character, the winglike condition of the incisors, and the protostylid polymorphism. These hypotheses generally involved dominant or recessive autosomal alleles with incomplete penetrance and manifold expressivity (e.g. Korkhaus, 1930; Dietz, 1944; Abrahams, 1949; Tsuji, 1958; Witkop, 1960; Dahlberg and Fukuhara, 1964).

Kraus (1951) initially supported a codominant, single autosomal locus mode of tranmission for the Carabelli trait, but found that a multi-allele, monogenic hypothesis was more appropriate after further research (Kraus, 1959; Kraus et al., 1969:297). Dahlberg et al. (1956) and Devoto et al. (1968) suggested that a similar multi-allele system might control the expression of the shovel-shape character on the upper incisors. Other workers have proposed codominant, unifactorial models to explain the inheritance of attributes like the protostylid and shovel-shape features (Devoto et al., 1972; Portin and Alvesalo, 1974).

Turner (1967a,b:9-10; 1969a), following Kruas (1951), proposed a model of two codominant alleles at a single autosomal locus to accuont for the phenotypic variation seen in several crown features, e.g. the shovel-shape character, hypocone reduction, the Carabelli complex, and the protostylid polymorphism. One allele would act as a phenotype-intensifier and the other as a phenotype-suppressor, producing three basic categories of attribute manifestation: marked expression, intermediate forms (the heterozygous state) and trait absence. Turner applied this inheritance model to his study populations, viz. skeletal living Eskimo and Amerindian groups.

However, Turner did not use pedigree data to establish the mode of transmission of the feature used in his analysis of aboriginal dentitions. Instead, he assumed that the traits under examination were initially in a state of genetic equilibrium, so that expected allele frequences could be determinated for each character by applying the Hardy-Weinberg Law. The phenotype frequencies observed for each attribute in the study population were then tested against the expected Hardy-Weinberg distribution by means of the X^2 statistic. Because a significant difference was usually not found between observed and expected values, Turner concluded that the proposed codominant-allele hypothesis was a valid one in most cases. Other workers reported similar results, using the same model and the same method, for the features considered in their study samples (Cadien, 1966; Winton, 1966).

However, Sofaer (1970) demonstrated that the procedure used by Turner and others was critically flawed. The use of arbitrarily-defined genotypes with the Hardy-Weinberg Law is not a valid approach, because the law can only be applied to known trait loci in cases where the relationships of individuals are uncertain. This condition was not met in any of the studies which used Turner's method of testing the codominant model and reported usccessful results (e.g Cadien, 1966; Winton, 1966; Turner, 1967a,b:9-10; 1969a; Devoto et al., 1968; 1972).

The codominant, unifactorial hypothesis has been proved to be inadequate to account for the phenotypic distributions of dental features in samples where the relationships of individuals were known. Goodman (1965) demonstrated that Kraus' (1959) Carabelli complex data would not fit his (1951) inheritance model for this trait. Two major investigations tested the Kraus-Turner hypothesis, for the Carabelli complex in a population of 123 families, and for the shovel-shape character, hypocone reduction, and lower molar cusp-number and groove pattern in a population of 100 families (Goose and Lee, 1971; Lee and Goose, 1972). The conclusion drawn from this research was that simple Mendelian models involving dominant, recessive, or codominant alleles are not valid for the commonly studied crown attributes.

The use of complex developmental models to describe the transmission and manifestation of dental characters has become prevalent only in the last two decades. A few of the earlier workers proposed multifactorial hypotheses to account for their observations on attributes such as the Carabelli complex, protostylid polymorphism, entoconulid expression, and the shovel-shape feature (e.g. Dietz, 1944; Dahlberg, 1951; 1962; Oschinsky and Smithurst, 1960; Goodman, 1965). Most odontologists now accept a polygenic, quasicontinuous mode of inheritance for crown traits (e.g. Sofaer, 1970; Sofaer et al., 1972a,b; Scott, 1973:109-113; 1974; Bailit et al., 1974; Berry, 1976; 1978; Harris, 1976; Scott et al., 1983; Turner, 1985; Sofaer et al., 1986).

2.3 Methodology for Grimsby dental study.

Because one of the objectives of this thesis was to compare the Grimsby dentitions with those from Shaver Hill, Carton, Kleinburg and Sopher, it was necessary to make the methodology followed here as similar as possible to that followed by P.J. Wright (1974) and K.E. Wright (1977). Both used the photographs and definitions of Kraus et al., (1969), as well as written descriptions of features which they quoted or gave in the thesis text (Wright, 1974:210-

211; Wright, 1977:6,11). These standards were accepted and used in this work.

The dental morphological traits considered here are those believed to be of some use in population comparisons at the microgeographic level. A number of the traits employed by P.J. Wright and K.E. Wright were not used in this thesis because a lack of rating consistency was observed in the samples that were scored for these features. Others were so subjective that it seemed inappropriate to use them for any sort of interdemic comparisons. A certain degree of subjectivity is inevitable in morphological grading and description; however in the cases referred to above, the features were very subtle and the probability of gross interobserver error appeared to be very great. Other characters, such as root number, could not be recorded, except in a very few cases where the gnathic specimen had been broken.

The individual count method was used for all traits considered in the thesis. Individual genotypes are the real units constituting a population; side and tooth counts may underestimate gene frequencies for a trait by as much as 50% (Scott and Dahlberg, 1982). In practice, however, the three procedures usually yield closely comparable results, according to Scott (1980).

Observations were also given by sex; in cases of large discrepancies in trait frequencies between males and females, X^2 tests were utilized to determine the significance of the difference. Data were given for left and right sides for traits that were also scored by P.J. Wright and K.E. Wright. Both were dealing with ossuary populations, an so did not have the option of recording by individual count or establishing the sex of any of their specimens. They were forced to identify individual teeth as accurately as possible, using Kraus et al. (1969) for antimere classification.

The morphological features of interest in this study were scored with the aid of a magnifying glass (10X) and a strong light (150 to 300 watts). The observations were recorded for both sides of every specimen on the data sheets. If the presence or absence of a trait was not determinable for one or both sides, the specific reason for this situation was noted on the sheets.

Intra-observer error has increasingly been recognized as a problem in studies of skeletal features (Molto, 1983:103-112). P.J. Wright (1974:8-11) did not consider intra-observer error in his study; K.E. Wright (1977:11) did not determine it for individual traits, but estimated her error to be ca. 15% overall. Scott (Scott and Dahlberg, 1982) noted that his intra-observer error varied with the feature under consideration, from 3% to 10%.

In this study, standards were set up for every trait scored, and the more subjectively graded features, e.g.

shovel-shaping, maxillary molar cusp-number, Carabelli and protostylid traits, were rated twice for all specimens within a six month span. Intra-observer error was found to be between 5% and 10%, depending on the feature considered.

2.4 Terminology for Grimsby dental study.

The nomenclature and symbols employed in this study are basically those standardized by G.V. Black (1897:ix-xvii), as revised by Kraus et al. (1969:xiii-xv). The most commonly used of these terms are given in the following illustrations (see Figures 3a,3b,3c, pp. 31-33). The upper and lower canine have been designated "C^1" and "C_1", respectively, following while the primary molar cusps are referred to by the symbols "c_1 - c_5", after Scott and Dahlberg (1982), or by the Grecised names coined by H.F. Osborn (1888; 1892; 1907:40-41,63).

While the molar nomenclature has been widely accepted, there has been marked disagreement regarding how the Osbornian labels should be applied to premolar cusps (see Osborn, 1907:195-200,215-216; Gregory, 1922:103-104,513-515; Morris, 1965:33-39,51-58). This is particularly the case for the lingual convexities, for which W.B. Scott introduced the terms "deuterocone" (upper bicuspid), "deuteroconid" and "tetraconid" (lower bicuspid/tricuspid). The correct homologies for these elements are not certain (see Figure 3c, p. 33). Therefore, the simple

Figure 3a. Terminology for dental orientation.

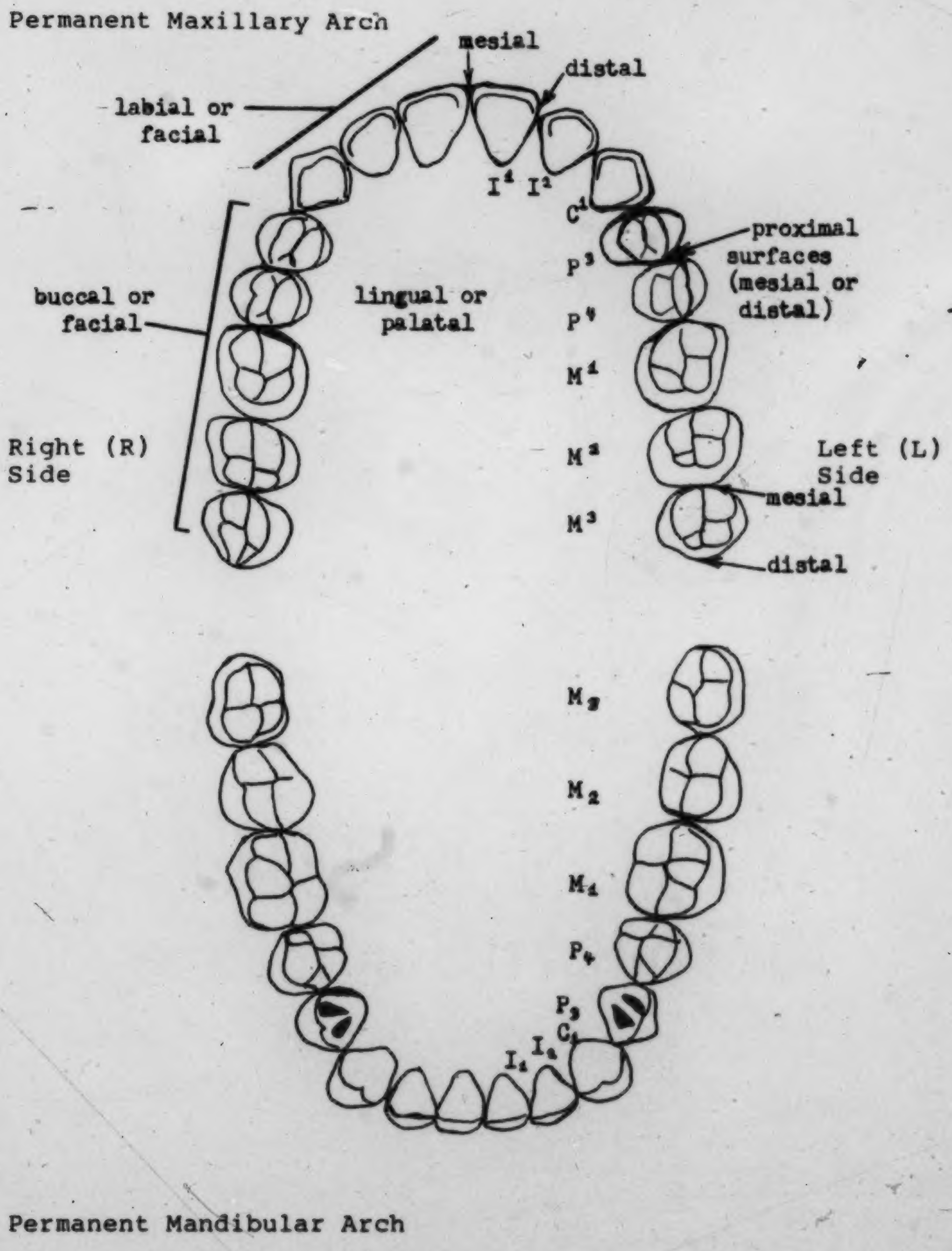
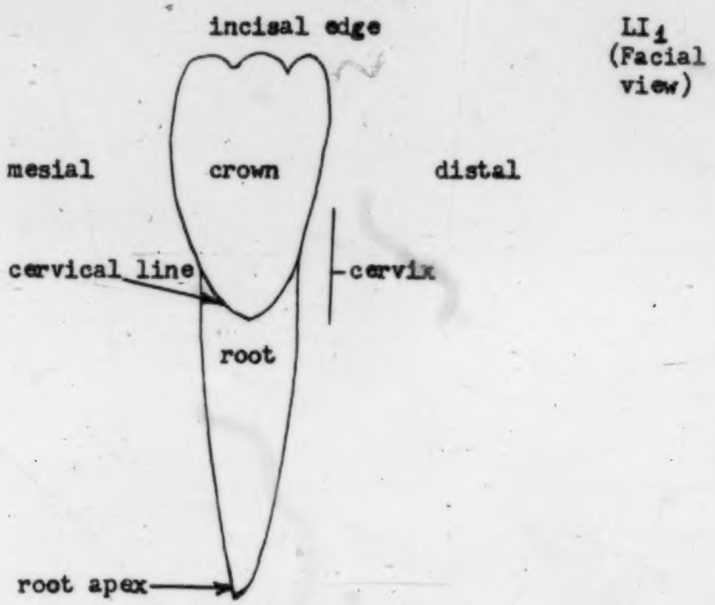

Permanent Maxillary Arch
mesial
distal
labial or facial
I^1 I^2
C^1
proximal surfaces (mesial or distal)
P^3
buccal or facial
lingual or palatal
P^4
M^1
Right (R) Side
M^2
Left (L) Side
mesial
M^3
distal
M_3
M_2
M_1
P_4
P_3
C_1
I_2
I_1
Permanent Mandibular Arch

Figure 3b. Terminology for dental anatomy: basic tooth features.


incisal edge
LI_1
(Facial view)
mesial
crown
distal
cervical line
cervix
root
root apex

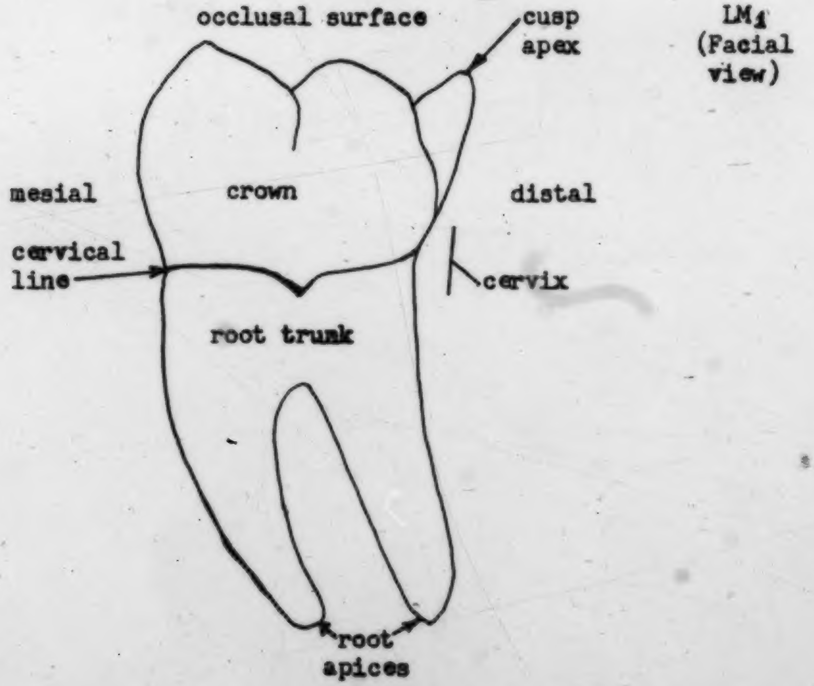
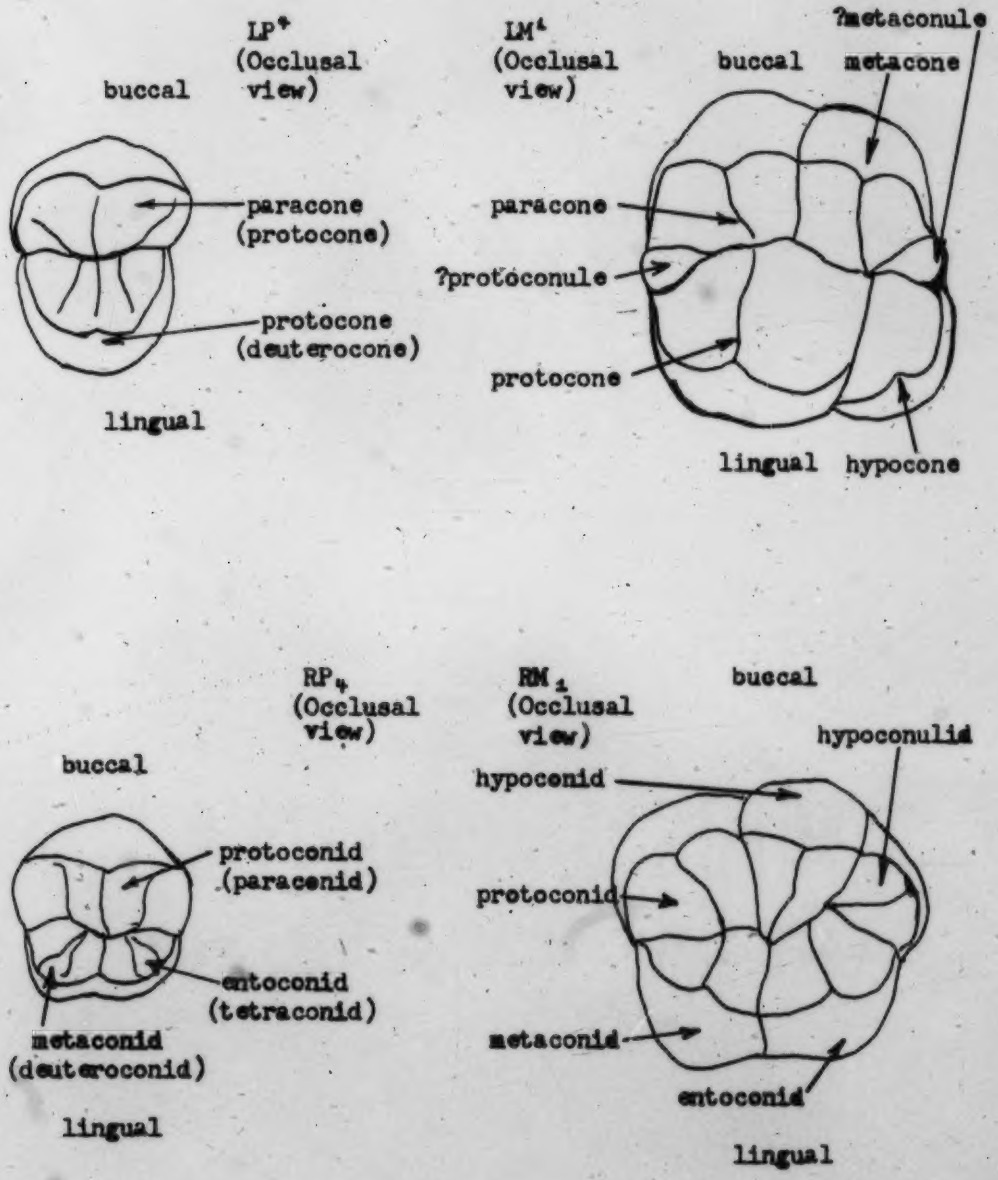

occlusal surface
cusp apex
LM_1
(Facial view)
mesial
crown
distal
cervical line
cervix
root trunk
root apices

Figure 3c. Terminology for dental anatomy: occlusal cusp nomenclature.


LP^4
(Occlusal view)
buccal
paracone (protocone)
protocone (deuterocone)
lingual
LM^1
(Occlusal view)
buccal
?metaconule
metacone
paracone
?protoconule
protocone
lingual
hypocone
RP_4
(Occlusal view)
buccal
protoconid (paraconid)
entoconid (tetraconid)
metaconid (deuteroconid)
lingual
RM_1
(Occlusal view)
buccal
hypoconulid
hypoconid
protoconid
metaconid
entoconid
lingual

expressions "buccal cusp" and "lingual cusp(s)" will be used here.

The traditional way of numbering the first and second bicuspids (viz. as P3 and P4) in the upper and lower jaws has been followed in the section dealing with that class of teeth. The belief that premolar loss occurred only at the locus nearest the canine goes back to Gregory's (1916:281, 284) seminal work on primate dentition. This idea became widespread during the interbellum period (Weidenreich, 1937a:4) and is the common assumption today (Schwartz, 1980; 1982).

It should be noted, however, that some workers do not agree with the traditional hypothesis. Weidenreich (1937a:4; 1945:28,43) had doubts about Gregory's thesis and referred to hominoid premolars as P1 and P2. Schwartz (1980; 1982) has presented palaeontological and embryological evidence against Gregory's presumed sequence of tooth loss. He believes that ceboid premolars, for instance, should be numbered P2, P4 and P5 rather than P2, P3 and P4. However, Jungers and Gingerich (1980) have concluded from studies of supernumerary teeth in living and extinct primates that Gregory's original interpretation was the correct one.

Many dental anthropologists have simply ignored palaeontological convention and numbered the two bicuspids as P1 and P2 in both jaws. These include such workers as: Suzuki and Sakai (1957); Garn et al. (1963); Bailit et al.

(1968); Le Bot and Salmon (1977); Wajeman and Levy (1970); Scott et al. (1983); Turner (1985; 1987). However, until further research elucidates the actual pattern of premolar loss and retention, it is probably less confusing to use the traditional way of designating these teeth.

Another problem is the use of Osbornian nomenclature to label certain accessory cusps, one of which sometimes appears on the anterior margin of the upper molars, and the other of which is found with some frequency on the posterior margin of the same teeth. The former tubercle ahs been referred to as the "protoconule" by some workers (e.g. Jørgensen, 1956:127-128; Lukacs, 1987) and the latter as the "metaconule" by several investigators (Jørgensen, 1956:128-129); Harris and Bailit, 1980; Noss et al., 1983; Lukacs, 1987). However, research by Korenhof (1960:201-204,239) indicates that the original primate protoconule and metaconule were probably lost early in hominoid evolution. Therefore, these two terms will not be used to describe anatomical features on human molars in this thesis.

CHAPTER 3.

MAXILLARY AND MANDIBULAR INCISORS.

3.1 Introduction.

This section will deal mainly with the anatomy, phylogeny, racial variation and genetic aspects of three dental attributes: the axial-rotation or "winging" feature, the shovel-shape character and the lingual tubercle expression. These traits have been widely used in the last half century for the descripton of Amerindian dentitions. Minor anatomical variations, viz. linguocervical grooves and labial incisor-form will also be considered in this chapter.

A high incidence of strongly shovel-shaped upper incisors has traditionally been considered a diagnostic raical trait for Mongolid populations (Hrdlička, 1920; Nelson, 1938; Goldstein, 1948; Dahlberg, 1951, 1963). Modern workers have consistently used this feature in bilogical distance analyses involving Amerindian and Eurasian samples (e.g. Scott, 1973:128,147; Brewer-Carias et al., 1976; Scott and Dahlberg, 1982; Turner, 1983; 1985; 1987). The labial-ridging character, which is usually associated with the shovel-shape expression, will be considered in the same subsection. It has been used recently in several studies dealing with demic comparisons of Mongoloid peoples (e.g. Turner, 1983; 1985; 1987).

Winglike incisors and lingual tubercles have both become widely used in biological distance analyses of Amerindian and other Mongoloid populations (e.g. Turner, 1983; 1985; 1987). Frequencies of these features are usually given for the upper anterior teeth, as they are much less important for the lower anterior elements. The lingual tubercle character is often associated with other cingular expressions, viz. ridges, grooves and pits; so all of these variations will be considered together in the same subsection.

Mandibular incisor traits are not as useful for biological distance analyses as maxillary attributes, but observations on a few of these characters will be given here. The shovel-shape variation of the lower incisors has been used as a descriptive and comparative feature by some workers (e.g. Morris, 1965:46; Turner, 1967b:25,35). Morris (1965:47) and Molto (1979:23,36) have noted the occurrence and possible diagnostic significance of axially-rotated central teeth.

Minor anatomical variations will be considered in a separate subsection at the end of the chapter. These include linguocervical grooves and labial shape of the upper incisors. Both characters have been studied by a few workers (e.g. Williams, 1914; Turner, 1987).

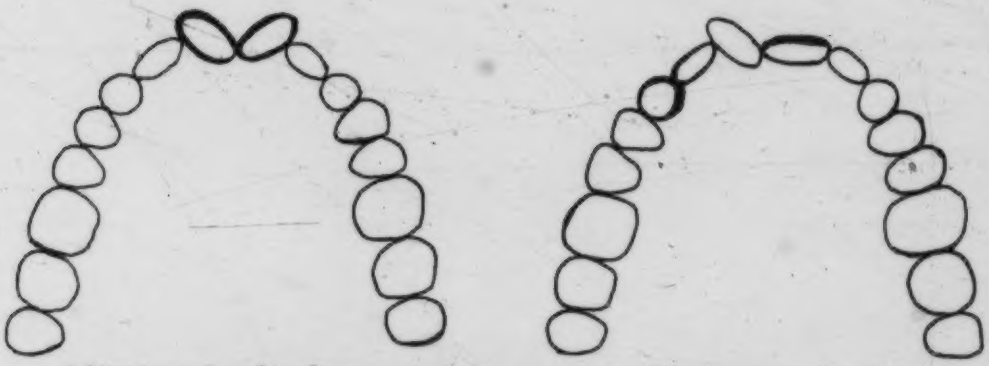
3.2 Winging trait of maxillary and mandibular central incisors.

3.2.1 Various aspects of winging trait.

The winging condition ("mesiopalatal torsion") occurs when the mesial edge of a central incisor is directed or "rotated" inwards (or lingually) and slightly backwards, while the distal edge is "rotated" outwards and slightly forwards, giving the tooth a winglike appearance (see Figure 4a,4b, pp. 38-39). The counterwinging form is found when the "rotation" is in the opposite direction, so that the mesial edge is directed outwards relative to the dental arch. The winging and counterwinging expressions may be unilateral or bilateral, so that four types of incisor orientation can be observed (Dahlberg et al., 1958; 1959; Dahlberg, 1963a).

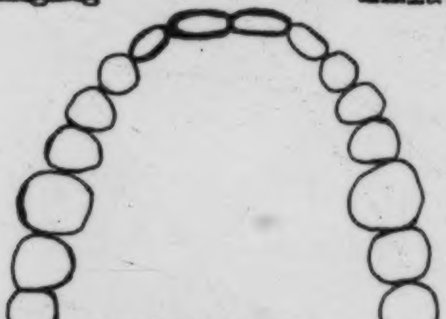
The first worker to describe winglike central incisors was Leigh (1928), who noted their presence in a prehistoric cranial series from California. Nelson (1938) found that bilateral mesiopalatal torsion occurred in 30% of the first upper teeth of his skeletal Pecos Pueblo population, and suggested that this feature might be of a racial and hereditary nature. Wright (1941) reported an even higher incidence of bilateral lingual rotation (46%) in the living Jivaro of Ecuador. However, the first major comparative study was made by Dahlberg et al. (1958, 1959); this included 10 American Southwest tribal groups as well as Euro-American and Japanese samples.

Figure 4a. Winging trait of central incisors: phenotypic variation. (Adapted from Turner, 1967b: 37a, Figure 3.)

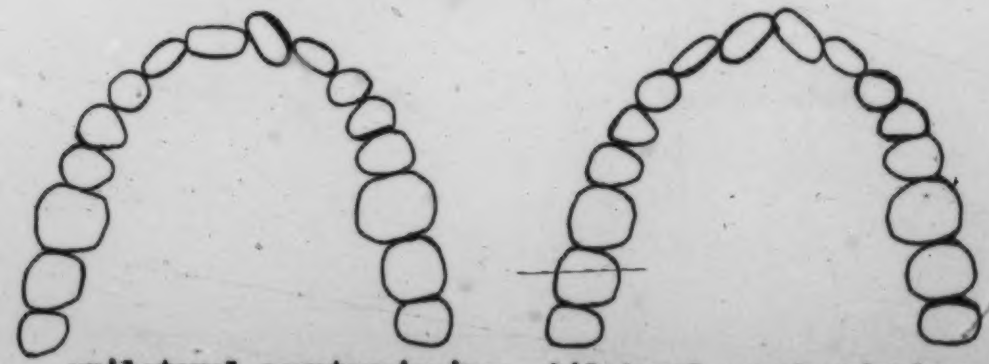


bilateral winging

unilateral winging



straight form

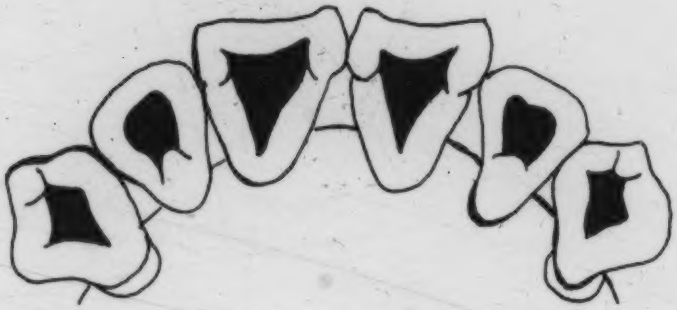


unilateral counterwinging

bilateral counterwinging

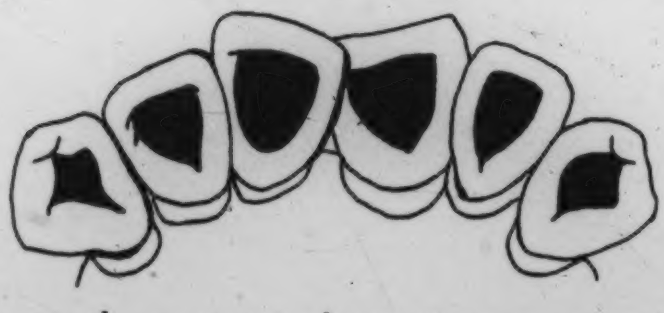
Figure 4b. Winging trait of central incisors: bilateral winging - Grimsby specimens.

straight form



Left I^1 and Right I^1 (Fe9#26: Lingual view)

bilateral winging



Left I^1 and Right I^1 (Fe62#61: Lingual view)

Mongoloid populations display regional patterns in the occurrence of different forms of mesiopalatal torsion. Small South American groups, mainly from Brazil, Chile and Ecuador, apparently show the highest frequencies of bilateral winglike incisors, ranging from ca. 25%-65%, and averaging ca. 55%, e.g. the Jivaro, Pewenche, Xavante (Wright, 1941; Niswander, 1967; Rothhammer et al., 1968; Campusano et al., 1972; Brewer-Carias et al., 1976; Turner, 1985). Tribal populations from the American Southwest also display notable incidences of the bilateral winging expression, c.a. 20%-40%, and generally somewhat lower incidences of the bilateral counterwinging condition, ca. 5%-30%, e.g. the Maricopa, Pima, Yuma (Dahlberg et al., 1958; 1959; Scott, 1973:159-160).

In contrast, Eskimo and northern Oriental samples (e.g. Chinese, Japanese) tend to manifest distinctly lower proportions of both bilateral lingual rotation, ca. 5%-20%, and the bilateral countertorsion variation, ca. 0%-15% (Dahlberg et al., 1958; 1959; Turner, 1967b:36-38; 1983; 1985). The winging trait is also less commonly observed among Southeast Asian and Polynesian peoples than among Amerindians. The former show frequencies of ca. 10%-35% for the bilateral winging phenotype and ca. 0%-5% for the bilateral counterwinging form, e.g. Burmese, Japanese Ainu and Jomon, Easter Islanders (Turner, 1979; 1985; 1987; Turner and Hanihara, 1977; Turner and Scott, 1977).

Mesiopalatal torsion of the upper central incisors is observed only rarely in most non-Mongoloid populations. Euro-American samples display very low frequencies of the bilateral winging expression, ca. 3%-5%, and much higher frequencies of unilateral and bilateral counterwinging expressions, ca. 15%-50% (Dahlberg et al., 1958; 1959; Scott, 1973:159-160; Mayhall et al., 1982). The Jat cranial series from northwestern India shows possibly the lowest incidence of bilateral lingual rotation on record (2%), and a complete lack of the other forms of axial rotation (Kaul and Prakash, 1981). Some New Britain Melanesian groups are unusual in that they manifest relatively high proportions of bilateral mesiopalatal torsion (ca. 20%), although the unilateral mesiopalatal and countertorsion variations are very seldom observed (Turner and Swindler, 1978).

While the winging trait has been used by several workers in biological distance comparisons of various populations (e.g. Rothhammer et al., 1971; Brewer-Carias et al., 1976; Scott and Dahlberg, 1982; Turner, 1983; 1985; 1987), very little research has been done on the nature of its inheritance. Witkop (1960) suggested than an autosomal dominant hypothesis could account for the phenotypes associated with axial rotation. The first large pedigree study indicated an autosomal dominant mode of transmission with incomplete penetrance and manifold expressivity (Escobar et al., 1976). However, most dental anthropologists would support a polgenic, quasicontinuous model of inheritance (Scott et al., 1983; Turner, 1985). Sexual dimorphism has not been observed for central incisor rotation (Turner, 1967n:36; Mayhall et al., 1982).

The assumption that a relatively high frequency of the bilateral winging expression can be considered a diagnostic racial attribute is complicated by the possibility that axial incisor rotation may involve two different factors: a genetic component reflecting Mongoloid affinities, and an idiosyncratic component, reflecting individual gnathic growth problems and resulting in the crowding of anterior teeth. In the former instance, mesiopalatal torsion would be the result of socket formation at an angle to the normal curve of the dental arch (Scott and Dahlberg, 1982). This appears to be the case in a study of over 1000 Japanese children (Dahlberg et al., 1958; 1959) in which nearly 10% of the subjects displayed the bilateral winging condition without any evidence of crowding (see also Nelson, 1938).

However, there are many examples of incisor rotation related to the physical pressure of anterior tooth crowding in the jaw. Scott et al. (1983) have noted that the counter-winging expression is usually associated with tooth crowding among American Southwest tribal groups. Molto (1979:23,36) remarked that mandibular incisor rotation is connected with tooth crowding in proto-Iroquois populations (e.g. at Donaldson and Serpent Mounds), although he also believed that this character reflects a genetic relationship at the demic level.

The current tendency among workers who use incisor rotation as a key trait in Amerindian studies is to utilize bilateral-winging frequencies and classify the other types of axial rotation with the normal state in the "absent" category (Scott and Dahlberg, 1982; Scott et al., 1983, Turner, 1983; 1985). This is done because bilateral mesiopalatal torsion seems to be influenced to only a minor degree by anterior tooth crowding and is therefore the most accurate genotypic indicator, of the several forms of central incisor rotation. It also appears that the bilateral winging variation occurs much more commonly than the unilateral winging and counterwinging expressions in the Amerindian populations that have been studied to date. Scott et al. (1983) have observed that the combined incidences of the other types of rotation constitute only a minor proportion (7%) of rotated central incisors in uncrowded dentitions.

3.2.2 Methodology for winging trait.

Central incisor rotation among the Grimsby specimens was classified according to the five-fold division proposed by Dahlberg et al. (1958) and illustrated by Turner (1967b:37a, Figure #3): bilateral winging, unilateral winging (left or right), normal state, unilateral counterwinging (left or right) and bilateral counterwinging categories (see Figure 4a, p. 38) All cases where crowding occurred were noted, and the frequencies of each type of incisor rotation were calculated for both upper and lower incisors.

Empty sockets were ignored in the tabulation of data for left and right sides; specimens with a socket on one side and a rotated or nonrotated tooth on the other were not included in the individual-count procedure. It was felt that the determination of the winging or nonwinging condition in the case of an empty socket could not be made with any certainty. The rather circular shape of maxillary central incisor sockets made this determination difficult if not impossible; while mandibular incisor sockets are rather oblong in form, slight rotation of a tooth crown would still be difficult to ascertain.

3.2.3 Observations on winging trait.

The observations on the Grimsby specimens are given in Tables 1a,1b, pp. 44-46. In the upper incisors, 18.2% (8/44) of the determinable specimens manifested some degree (usually slight) of unilateral mesiopalatal torsion, while only two individuals (Fe62#37 and Fe62#61) displayed the bilateral winging expression (4.5%) and only one (Fe15#1) the counterwinging variation. Of the total number of cases showing incisor rotation, only 20.0% (2/10) displayed any

TABLE 1a. WINGING TRAIT OF CENTRAL INCISORS IN GRIMSBY SAMPLE: OCCURRENCE BY SIDE.

SEX	MAXILLARY INCISOR		MANDIBULAR INCISOR	
	L SIDE	R SIDE	L SIDE	R SIDE
	#	#	#	#
MALE				
straight	17	15	16	18
unilat	3	5	2	0
counter	1	0	0	0
total	21	20	20	20
crowding	1	1	3	1
FEMALE				
straight	20	23	13	9
unilat	2	2	2	3
counter	0	0	0	2
total	22	25	19	18
crowding	1	1	4	8
ALL				
straight	42	42	33	33
unilat	5	8	7	3
counter	1	0	0	2
total	48	50	48	46
crowding	2	2	10	10

TABLE 1b. WINGING TRAIT OF CENTRAL INCISORS IN GRIMSBY SAMPLE: OCCURRENCE BY INDIVIDUAL.

SEX	MAXILLARY INCISOR INDIV+ # (%)	MANDIBULAR INCISOR INDIV+ # (%)
MALE		
straight	12 (63.2)	14 (77.8)
unilat	6 (31.6)	2 (11.1)
bilat	1 (5.3)	2 (11.1)
counter	0 (0.0)*	0 (0.0)
total	19 (100.0)	18 (100.)
crowding	1	3
FEMALE		
straight	19 (90.5)	7 (43.8)
unilat	1 (4.8)*	4 (25.0)*
bilat	1 (4.8)	4 (25.0)
counter	0 (0.0)	1 (6.3)*
total	21 (100.)	16 (100.)
crowding	1	7
ALL		
straight	34 (77.3)	25 (59.5)
unilat	8 (18.2)	8 (19.0)*
bilat	2 (4.5)	8 (19.0)
counter	0 (0.0)	1 (2.4)
total	44 (100.)	42 (100.)
crowding	2	12

+ Counts only include specimens with both sides scorable.

* Specimen showing winging or counterwinging expression on one tooth excluded from count due to absence of opposing antimere.

significant indication of crowding (viz. Fe62#37 and Fe62#61); this was demonstrated by the rotation of lateral incisors or canines, or by the occurrence of deeply concave interproximal wear facets on the anterior teeth. There was some indication of sexual dimorphism: only 9.5% of females showed winglike central incisors compared to 36.8% of males. It is interesting to note that in the most crowded dentary (Fe62 #20), there was no rotation of the central incisors; instead, they were pushed outwards or labially from the rest of the arch.

Mesiopalatal torsion was much more commonly found in the mandibular incisors. The unilateral winging expression occurred in 19.0% (8/52) of the determinable casts; the bilateral winging variation in 19.0% (8/42) and the unilateral counterwinging form in 2.4% (1/42). Crowding was evident in 70.6% of all cases of rotation (12/17); if all individuals scorable on one or both sides are considered, the frequency would rise to 75.0% (15/20, including both counterwinged specimens). Of the individuals showing crowded anterior teeth, 60.0% (9/15) displayed rotation of either the lateral incisor or the canine. There was some indication of sexual dimorphism: 56.3% of the females manifested some type of axial rotation, compared to 22.2% of the males.

3.3 Shovelling trait and labial -ridging character of maxillary and mandibular incisors.

3.3.1 Anatomical description and phylogeny of shovelling trait on maxillary incisors.

The most intensely studied incisor trait has been the shovel-shape character. The term refers to the presence of strongly elevated ridges on both mesial and distal margins of the lingual surface (see Figures 5a,5b, pp. 49-50). The ridges, which are composed both enamel and dentine, given teeth of this kind a scoop-like appearance. A lingual fossa is formed beteen the two marginal ridges; it should be noted that this feature is not an actual depression in the surface but occurs as a result of the build-up of the ridges (Weidenreich, 1937a:22; Tratman, 1950a; Mayhall, 1972).

Mühlreiter was apparently the first worker to describe lingually-ridged incisors as resembling a shovel (in 1870; cited by Hrdlicka, 1920). However, Hrdlicka (1907; 1908:124) popularized the term "shovel-shaped incisors" and was the first to point out its significance as a racial trait characteristic of Mongoloid populations, especially Orientals and Amerindians. He also proposed (1920) a usable, albeit somewhat subjective scale, which rated the degree of shovel-shape expression according to four grades: nonshovel, trace shovel, semishovel and shovel or full shovesl (see Figure 5a, p. 49). Strongly shovel-shaped incisors had pronounced ridges and a "deep" lingual fossa; moderately shovel-shaped teeth had much weaker ridges and a

Figure 5a. Shovelling trait of maxillary incisors: phenotypic variation.

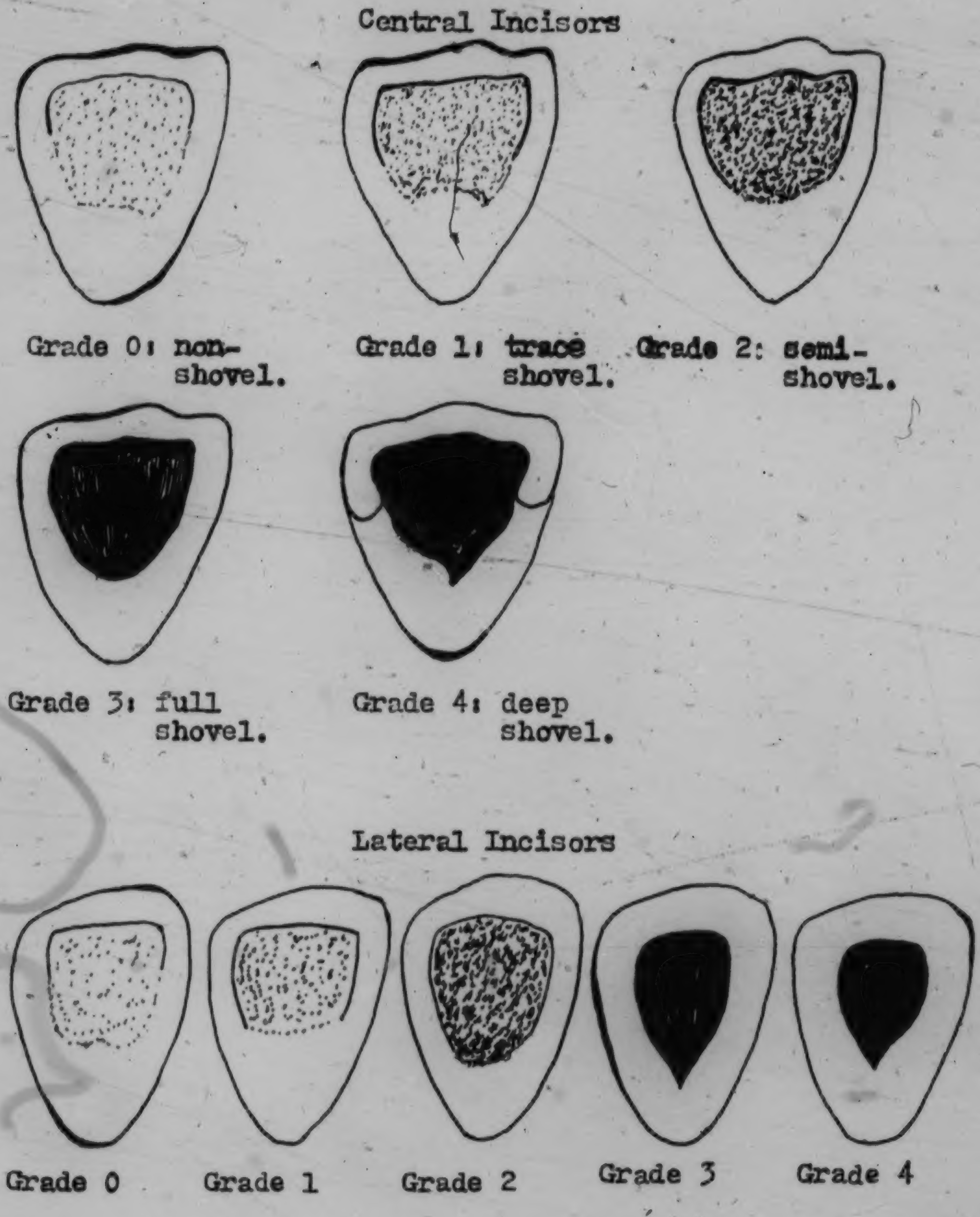
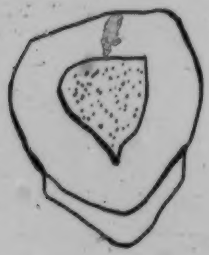
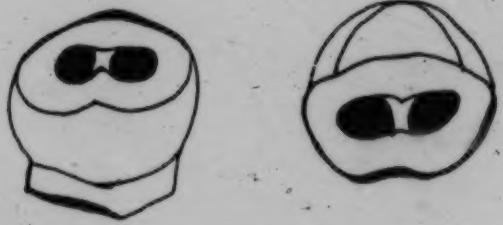

Central Incisors
Grade 0: non-shovel.
Grade 1: trace shovel.
Grade 2: semi-shovel.
Grade 3: full shovel.
Grade 4: deep shovel.
Lateral Incisors
Grade 0
Grade 1
Grade 2
Grade 3
Grade 4

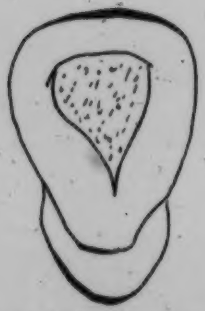
Figure 5b. Shovelling trait of maxillary incisors: barrel-shaped variation - Grimsby specimens.



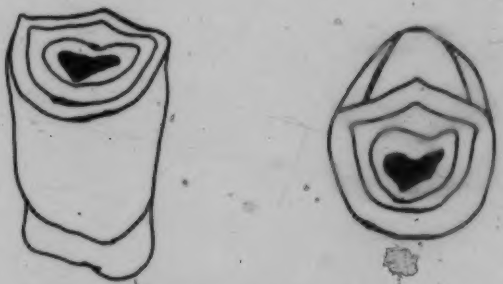
Deep-shovel antimere.



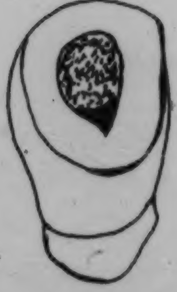
Barrel-form antimere.



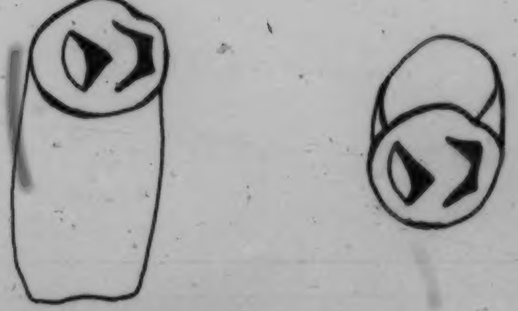
Full-shovel antimere.



Barrel-form antimere (worn).



Quasibarrel antimere.



Barrel-form antimere (compressed).

"shallow" fossa, and slightly shovel-shaped elements had distinct but narrow ridges along both borders and a faint depression. Incisors with little or no trace of the ridge and fossa formation were placed in the "nonshovel" or "absent" category.

The two maxillary incisors (I^1 and I^2) usually manifest the same degree of the shovelling trait (Hrdlicka, 1920; Carbonell, 1963). However, Hrdlicka (1920) noted that in south-central Oriental populations (Chinese, Japanese) the central incisor had higher frequencies of marked shvelling, while in northern and American Mongoloids (Amerindians, Eskimos, Mongolians), the lateral tooth had higher proportions of the pronounced phenotype. Dahlberg (1951) reviewed the data then available on lingual ridging in different racial groups and came to the conclusion that the central incisor generally displayed a greater incidence of the full-shovel grade than the lateral element. A decade or so later, Carbonell (1963) came to the opposite conclusion after making a similar compilation of studies.

More recent research on Mongolid and non-Mongoloid peoples has not yielded consistent results. In Turner's (1967b:25,29) analysis of Arctic Mongoloid dentitions, the lateral incisor showed a distinctly high frequency of marked shovelling than the central tooth. However, Scott (1973:153-156) found that the first incisor (I^1) consistenly displayed a higher incidence--usually, twice as great as the second incisor (I^2) incidence--of the stronger degrees of shovelling expression in 10 American Southwest tribal populations. Richards and Telfer (1979) compared 6 Australarian groups and found that either tooth could show greater total-trait occurrence (marked shovelling was rarely manifested), depending upon the group considered. Berry's (1976) study of 8 skeletal and modern European samples supports the same conclusion.

One of the problems in comparing the two teeth is that shovel-shape expression in the narrower lateral incisor is likely to appear more pronounced when the lingual ridges are actually of the same height as in the wider central element (Moorrees, 1957:28; Bang and Hasund, 1971). According to Kirveskari's (1978) data, the second incisor in his Skolt Lapp sample displayed a higher frequency of the shovelling trait than the first one, but the mean fossa depth was distinctly greater in the latter. Scott et al. (1983) solved the difficulty of rating error due to tooth shape by using two different shovel-grade scales for the two maxillary incisors.

Barrel-shaped incisors have been linked to shovelling, as the strongest expression of the trait by a number of workers (e.g. Dahlberg, 1951; Lasker and Lee, 1957; Turner, 1967b:24-26; Bass, 1971:216,235; Baume and Crawford, 1978; 1980; Keiser and Preston, 1981; Scott et al., 1983). The barrel form occurs when there is an incisal "overgrowth" of the lingual cingulum which meets the lingual "overgrowth" of the marginal ridges on both sides to form a more or less cylindrical tooth with a depression in the centre (see Figure 5b, p. 50). The cingular "overgrowth" may reach two-thirds the length of the crown or more, sometimes extending to the incisal edge (Dahlberg, 1951; Bass, 1971:216; Mayhall, 1972). Maxillary lateral incisors are usually the only anterior teeth to display the barrel form; it is never very common (generally under 10%) and may occur unilaterally or bilaterally (Dahlberg, 1951; Scott, 1973:153-156).

There is some disagreement about the relationship between shovel-shaped and barrel-shaped incisors. Mayhall (1979b) was rather skeptical about this connection, and noted the discontinuity between full-shovel grade and barrel-type incisors in his Central Arctic Eskimo sample. Morris (1965:28-29) considered the barrel form to be an anomalous variation, as have other workers (e.g. Goaz and Miller, 1966; Niswander, 1967; Chung et al., 1972; Escobar et al., 1977; Mizoguchi, 1985:4,10).

However, barrel-shaped teeth are not found in populations which lack or have very low frequencies (ca. 1%) of marked and intense shovelling on the lateral incisors. This has been demonstrated to be the case for a number of diverse groups of African, European, Oriental and Australasian origins (Suzuki and Sakai, 1964; Turner, 1979; Turner and Hanihara, 1977; Turner and Swindler, 1978;

Mayhall et al., 1982; Kieser, 1984). Mayhall's (1979b) Eskimo samples showed a low proportion of marked shovelling (ca. 5% on the I^2), no evidence of intense shovelling, and only rarely displayed the barrel form (ca. 1%).

Barrel-type incisors occur much more commonly (5% - 20%) in populations manifesting high frequencies of marked and intense shovelling (70% - 80%), e.g. Kodiak Eskimo, several American Southwest tribes (Indian Knoll, Navajo, Papago, Pima, Pueblo) and a number of South American groups (Dahlberg, 1951; Goaz and Miller, 1966; Turner, 1967b:34; Niswander, 1967; Sofaer et al., 1972b; Scott, 1973:155; Keiser and Preston, 1981). Apparently, there is some sort of relationship between the proportions of the stronger trait expressions and the appearance of the barrel form (Epling and Dahlberg, 1956). A recent study indicates that an almost continuous range of variation exists between nonshovel-shaped incisors and barrel-form teeth in some Amerindian demes (Scott et al., 1983).

Some workers have suggested that the shovel-shape form and the peglike form (of I^2) are at opposite ends of the same phenotypic continuum, i.e. they belong to the same trait complex (Kirveskari, 1974:17; Mayhall, 1979b). However, pedigree analysis and statistical testing have demonstrated that conical elements are anomalous variations associated with congenital absence of teeth (Thomas, 1926; Keeler, 1935; Montagu, 1940; Grahnen, 1956; 1957; Niswander and Sujaku, 1963; Alvesalo and Portin, 1969; Woolf, 1971; Chung et al., 1972; Le Bot and Salmon, 1977; Brook, 1984). There is no good evidence to support the notion that peglike incisors are related to the shovelling trait.

The shovelling trait has been found in several anthropoid forms besides man, including some Old World monkeys and apes (Hrdlicka, 1920). The upper incisors of the gorilla and orang show pronounced lingual marginal ridges, while those of the chimp manifest only weak ridges. On the gibbon, the feature is virtually absent from the anterior teeth (Remane, 1960:783-784).

The shovel-shape character appears quite early in hominid evolution. Several australopithecine specimens (I^1 and I^2) from East African and South African sites (e.g. Hadar, Sterkfontein, Swartkrans) display weak or moderate shovelling (Robinson, 1956:23-29, 34; Johansen et al., 1982; Kimbel et al., 1982; Mizoguchi, 1985:46-47). The central and lateral upper incisors of the Choukoutien pithecanthropines show a pronounced shovel-shape expression (Weidenrech, 1937a:22-23, b:Plates 1-2). The anterior teeth of several neanderthal crania show some degree of lingual ridging, which varies from slight to robust, e.g. Ehringsdorf, Krapina, Le Moustier, La Quina, Vindija (Gorjanovic-Kramberger, 1907; Weidenreich, 1937a:23, b:Plate 3; Mizoguchi, 1985:43-46). According to Brabant's (1971) data, the incidence of marked shovelling was much higher on the upper incisor (especially on I^2, ca. 10% - 15%) in Neolithic and Megalithic French and Swiss populations than in modern Europeans.

The functional significance of reinforced lingual marginal ridges has been a matter of some debate. Hrdlička (1920) suggested that this feature served to strengthen the incisor, thereby increasing its durability. Dahlberg (1963b) has reported evidence which indicates that the shovel-shape structure resists breakage due to crushing or chewing. Turner (1983, 1985) proposed that the development of a number of "Sinodont" characters which increase tooth mass (e.g. pronounced shovelling) was an adaptive response to the harsh dietary regime that proto-mongoloid populations had to endure during the Pleistocene in morthern Asia. Mizoguchi (1985:110-113) concluded from an extensive study that the shovel-shape variation was a component of the mongoloid facial structure which served to resist strong biting forces related to meat-eating habits.

Other workers rejected the hypothesis that minor anatomical features could serve any critical purpose in the human dentition. Both Weidenreich (1937a:160-161) and Lasker (1945) felt that crown characters were not generally subject to selective pressures. Many modern odontologests have also become skeptical about the supposed functional advantages of dental variations (e.g. Scott et al., 1983; Turner, 1987).

3.3.2 Racial and geographic variation of shovelling trait on maxillary incisors.

Several investigations followed Hrdlička's original (1920) research, and examined skeletal and living populations of various racial affinities. Amerindians and Orientals were found to have the highest frequencies of strongly shovel-shaped incisors, by a large margin; these ranged from ca. 70% to ca. 100% among Amerindians and from ca. 60% - ca. 80% among Mongolians, Chinese and Japanese (Hrdlička, 1920; 1931; Wissler, 1931; Nelson, 1937; Lasker, 1945; Goldstein, 1948; Dahlberg, 1951). Eskimoid populations usually manifested lower frequencies of strongly shovel-shaped incisors than Amerindians; Alaskan groups showed incidences of 40% to 60% (depending on whether I^1 or I^2 was being considered), East Greenland natives ca. 85% and Aleuts ca. 60% - 65% (Hrdlička, 1920; Pedersen, 1949:185; Moorrees, 1957:24-25).

Heterogeneous groups, e.g., Hawaiians and American Chinese, had moderate frequencies (35% to 40% and ca. 20%) of strongly shovel-shaped teeth (Hrdlička, 1920; Lasker, 1945). American Caucasoid and Negroid populations had much lower incidences (0% to 5%) of marked shovelling (Hrdlička, 1920; Koski and Hautala, 1952; Lasker and Lee, 1957).

However, it became obvious that many of these early studies were not closely comparable, due to individual differences in morphological judgment. Stevenson (cited by Lasker, 1945) reported an unusually low value for strongly shovel-shaped incisors (8% to 10%) among North Chinese groups, although his semishovel category was rather large (ca. 50%). Carr's (1960) figures on early Minoan incisors showing marked shovelling were aberrantly high (27% on the I^1) for a presumably Caucasoid population. This problem led Dahlberg (1951) to suggest combining the full-shovel and semishovel or "moderate" categories, when interdemic comparisons were being made with data from different workers, so that interobserver error might be reduced, a procedure which has been followed by Oschinsky and Smithurst (1960), Suzuki and Sakai, 1964; Wajeman and Levy, 1978; Kaiser and Preston (1981).

In an attempt to create a more objective guide for shovel-shape classification, Dahlberg and Mikkelson (1947) used a modifed Boley gauge to measure the depth of the lingual fossa at its perceived midpoint a procedure later followed by Carbonell (1963) and Barner (1969), Kirveskari, (1974:18) and Mizoguchi (1985:16-17). In the mid-1950's, Dahlberg and Zoller Laboratory produced the first of a series of standard plaster plaques; the initial dental plaque depicted the four grades of Hrdlicka's system, plus the deep shovel-shape form, using casts of real specimens (Dahlberg, 1956).

This standard plaque has been widely adopted in the last three decades, during which the amount of dental research has been greatly expanded. Carbonell (1963) published a study of a number of European, Indo-Arabic, East Asian and Arctic populations, and gave a summary of the available data on shovelling of the incisors. Brabant (1971) has worked on Neolithic and Megalithic French and Belgian remains; Mayhall et al. (1982) have examined modern Canadian Caucasoids. Kirveskari (1974) worte a thesis on the dentition of the Skolt Lapps of northern Finland. Lee and Goose (1972) studied shovelling in a Liverpool Chinese community; Barnes (1969) described the trait in the Ugandan Teso tribe and Kieser (1984a) in the South African Griqua dentitions.

Asio-Indian populations, e.g. the Bhutanese (Prakash et al., 1979) and the Afghan Tajik (Beynon, 1971) have also been investigted for the shovel-shape feature. Several different Japanese groups have been studied, in particular the ancient Jomon (Turner, 1979), the modern Ainu (Turner and Hanihara, 1977) and the modern Janpese (Suzuki and Sakai, 1966), in relation to incisor shovelling, and so have extent Polynesian and Melanesian peoples (Suzuki and Sakai, 1964; Turner and Swindler, 1978).

A great amount of work has been done on American Mongoloid populations. Alaskan Eskimo groups have been studied by Turner (1967b; 1969a; 1983) and Bang and Hasund (1971); Aleutian Islanders by Turner (1967b; 1969a; 1983) and Central Eskimo remains by Mayhall (1979a,b); and figures for shovel-shape categories published in each case.

Shovelling in northern Athapascan dentitions has been investigated by Turner (1969a; 1983). A number of studies have been made on Southwestern Amerindian groups (Morris, 1965; Scott, 1973; Scott and Dahlberg, 1982; Scott et al., 1983) in which shovelling frequencies have been given. Several different native tribes of Central and South America have been examined for the trait (Devoto and Arias, 1967; Kieser and Preston, 1981) and values for a "hybrid" Chilean sample have also been reported (Pinto-Cisternas and Figueroa, 1968).

These investigations have usually tended to confirm the studies of earlier workers. However, some very low frequencies of strongly shovel-shaped incisors have been reported by Mayhall (1979b) for central Eskimos (5% to 10%) and some rather high ones, for total incidence in a Caucasoid sample (90% to 97%), by Sofaer et al. (1986). In general, the results support the belief that strongly shovel-shaped incisors are very commonly found in Oriental and Amerindian populations (50% - 100%) and rather rarely in modern Caucasoid and Negroid groups (0% - 5%).

3.3.3 Lateral asymmetry and genetic aspects of shovelling trait.

Previous to Harris' (1980) study, the mode of inheritance of the shovel-shape trait was generally considered to be autosomal. Tests for sexual dimorphism based on small or medium-sized populations usually failed to indicate any significant degree of difference. Abrahams (1949) found that a recessive Mendelian model was adequate to account for shovelling variation on a present/absent basis, in his South African Cape Malay population.

Turner (1967b:27-29; 1969a) proposed that the three basic degrees of shovelling could be accounted for by a codominant (two) allele system, and found that the observed phenotypic frequencies for the upper incisors (especially I^2) of his Arctic Mongoloid sample were not significantly different from the expected Hardy-Weinberg distributions. Devoto et al. (1968) used a similar method to test the two-allele hypothesis against their data from a northwestern Argentinian population. They found that the actual phenotypic proportions did not agree with the predicted Hardy-Weinberg values, and concluded that a multi-allele, single locus model might be more appropriate for the trait. However, this approach has since been demonstrated to be invalid (Sofaer, 1970).

Many researchers now believe that the mode of inheritance of the shovel-shape trait is polygenic. Suzuki and Sakai (1966) stated that shovelled incisors were probably the end product of a very complex genetic and ontogenetic interaction. Portin and Alvesalo (1974) concluded from their analysis of a Finnish population of known individual relationships that a presence of absence of lingual ridging on the upper central incisor could be explained by a polygenic hypothesis; a multi-allele, single-locus model; or a codominant allele system. Scott (1973:109,118) and Harris (1976) have suggested that the best explanation for the phenotypic distributions found in intrafamilial and interdemic studies would be provided by a continous or quasicontinuous polygenic model with a single phenotypic threshold. This now appears to be the general consensus of opinion (Scott et al., 1983).

Research on sexual differences in trait incidence has suggested that strong shovelling occurs more commonly in males of particular population (Hrdlička, 1931; Goldstein, 1948; Moorrees, 1957; Turner, 1967b; Pinto-Cisternas and Figueroa, 1968; Lee and Goose, 1972; Mayhall, 1979b; Mayhall et al., 1982; Harris, 1980). Kieser's (1984a) Griqua sample showed no consistent differences between the sexes. Dahlberg's (1951) Pima group and Barne's (1969) Teso were exceptional in that females displayed higher frequencies of full-shovel grade teeth.

However, Harris (1980) has demonstrated that upper incisor shovelling (on a present/absent basis) generally has a higher incidence in females than males. In the case of the maxillary central tooth, females exhibited higher frequencies than males in 28 out of the 38 populations considered (74%), while 12 samples (32%) showed statistically significant sex differences (at the $x^2p <0.05$ level). When these populations were combined into six main racial groups, viz. Caucasoids, Afro-Americans, Asians, Polynesians, Melanesians, and Amerindians, totalling some 19,000 individuals, significant sex differences (at the X^2p <0.02 level) were found in all divisions, except for the Afro-American. The degree of sexual dimorphism was found to vary with the geographic race under consideration. Similar results were obtained for the maxillary lateral incisor, except that the degree of sexual dimorphism was more pronounced.

Harris (1980) has recently proposed that incisor ridging is controlled by several X-linked loci. He also suggests that the greater shovel-shape frequencies observed in the females of several racial groups are the result of trait enhancement due to the presence of the double X chromosome in dental somatic cells. However, most workers continue to regard the shovelling feature as an autosomal attribute (e.g. Scott et al., 1983).

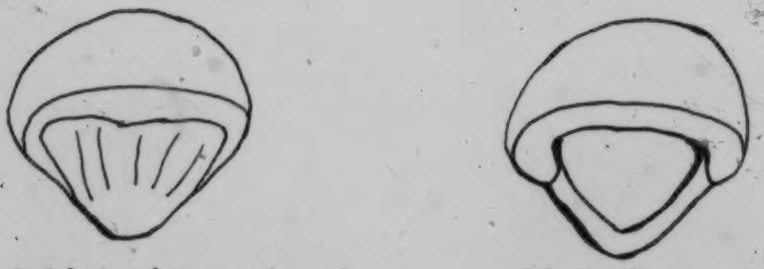
Lateral asymmetry in shovel-shape expression of the upper incisors is rare in all populations studied to date. When it occurs, it is usually associated with the lateral incisor (Hrdlička, 1920; Moorrees, 1957:23; Carbonell, 1963; Pinto-Cisternas and Figueroa, 1968; Mayhall, 1979b). Baume and Crawford (1980) found that asymmetry frequencies were generally under 5% for the first incisor and between 10% and 20% for the second one in their Mexican and Belizean groups.

3.3.4 Various aspects of labial-ridging character on maxillary incisors.

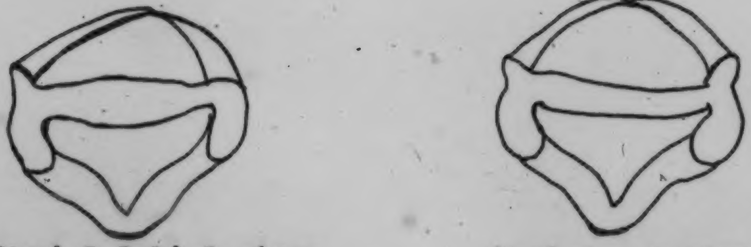
Labial incisor ridging was first noted by Muhlreiter (in 1891, cited by Hrdlička, 1921). Strongly shovel-shaped teeth with prominent mesial and distal facial ridges were orgianlly illustrated and described in Hrdlicka's (1920) seminal paper (see Figure 6, p. 65). These were later referred to as "double-shovels" by Dahlberg (1951). Single-margin labial ridging on shovelled incisors has been termed "three-quarter double-shovelling" by Snyder (1960) and "three-quarter shovelling" by Turner (1967a:25). Facial ridging occurs much less frequently and to a much weaker degree than lingual shovelling (Hrdlička, 1920; 1921; Moorrees, 1957:26; Snyder, 1960; Turner, 1967b:25,29; K.E. Wright, 1977:34,40).

Labial ridging is mainly found on the upper teeth of Mongoloid populations and tends to be rare or absent on the lower antimeres (Moorrees, 1957:26; Suzuki and Sakai, 1966; Turner, 1967b:29, 32; K.E. Wright, 1977:34,40). The most common manifestation is double marginal-ridging (of the "double shovel") which is most often displayed by the central incisors (Snyder, 1960; Turner, 1967b:29-30). Eskimo groups are exceptional in this regard; they show higher overall frequencies for mesiofacial ridging, which occurs most commonly on the lateral incisors in all populations (Turner, 1967b:30).

Figure 6. Labial-ridging character of maxillary incisors.



Labial ridges absent. Labial ridges absent.



Mesial labial ridge present. Mesial and distal labial ridges present.

Distofacial shovelling is rarely observed; it was noted by Moorrees (1957:26) in his living Aleut groups but was absent in all Turner's (1967b:29,32) skeletal samples (Aleut, Eskimo and Athapascan). Jomon and Griqua dentitions display low incidences of double and mesial labial ridging, but not distal ridging on either upper incisor (Turner, 1979; Kieser, 1984a). Double shovelling occurs in much higher frequencies in Amerindian groups (ca. 20% to 30%) than in Eskimo-Aleut groups (ca. 5% to 10%) on the central incisors (Snyder, 1960; Turner, 1967b:33).

There has been some disagreement over the connection between the frequency of labial ridging and the degree of shovelling most commonly found in a particular Mongoloid population. Moorrees (1957:26) remarked that in his Aleut sample there was no obvious association between the occurrence of facial ridging and the presence of deep or full shovelling. However, Suzuki and Sakai (1966) found such a relationship in their study of modern Japanese.

Turner (1967b:33-34; 1979; 1983; 1985; 1987) has considered labial ridging separately from the lingual-shovelling expression. Kieser and Preston (1981) have followed Turner in this regard, in their study of the Paraguayan Lengua tribe, but concluded that a high incidence of facial ridging is invariably accompanied by the dominance of full-shovel or deep-shovel grade teeth. It has been suggested that prominent lingual and labial ridging has served to strengthen and prlong the crown utility of the incisors of Amerindian and Arctic populations under dentally-demanding conditions (Dahlberg, 1963b; Turner, 1985).

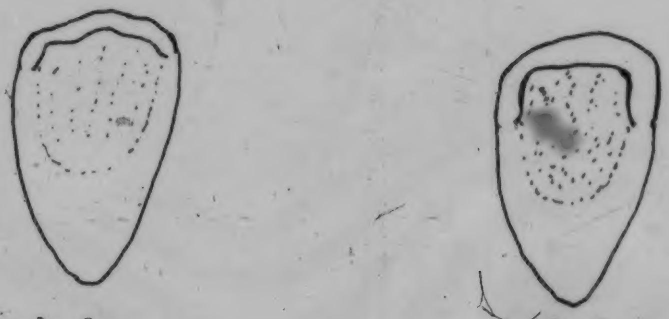
3.3.5 Various aspects of shovelling trait on mandibular incisors.

Shovel-shape expression is always much weaker on the lower anterior teeth (see Figure 7, p. 68). The full-shovel grade is rarely observed, and never reaches the degree of robusticity found on the upper incisors, even in Amerindian populations (Goaz and Miller, 1966). Total trait incidences for the central and lateral incisor for several American Southwest tribal groups range from 85% - 100% (Scott, 1973:156-159).

3.3.6 Methodology for shovelling trait.

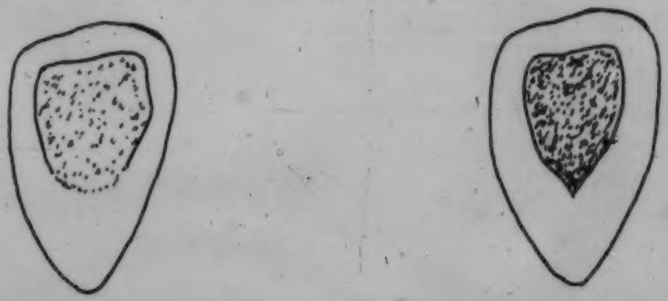
The procedures followed by P.J. Wright (1974) and K.E. Wright (1977) in their work on Iroquoian dentition were considered in establishing the methodology used for the Grimsby sample. P.J. Wright's (1974:18-19) rating system was very similar to Carbonell's (1963); both were based on Dahlberg's and Mikkelsen's (1947) technique of measuring the lingual fossa at its perceived center. One problem with this method is that lingual tubercles (and lingual enamel ridges) often interfere with the taking of accurate measurements (Lasker, 1950; Dahlberg et al., 1956;

Figure 7. Shovelling trait of mandibular incisors.



Grade 0:
nonshovel.

Grade 1:
trace shovel.



Grade 2:
semishovel.

Grade 3:
full shovel.

Carbonell, 1963). Another difficulty is that the presence of strong wear across the points of measurement prevents the correct evaluation of fossa depth, although unworn portions of the lingual ridges may clearly indicate the degree of shovelling (Goaz and Miller, 1966). It should be noted that Scott (1973:23-24), Scott and Dahlberg (1982) and Scott et al. (1983) have abandoned the metric classification technique in favour of a uniform-interval eight-grade scale, displayed on a standard plaster plaque.

K.E. Wright (1977:14-15) utilized Dahlberg's standard plaque P#1, which represented Hrdlička's four-degree system, and checked her scoring for a small tooth sample against that of J.T. Mayhall, an experienced worker in dental anthropology. (Their ratings differed by a grade at the most). Wright also added three categories to the traditional scale: deep-shovel grade incisors, peg and barrel-shaped elements.

The scoring of the shovel-shape trait for the Grimsby specimens was hampered by the fact that neither the new eight-grade plaque nor the old four-grade one was available at the University of Alberta. In their absence, some of the Grimsby casts were set up as standards to minimize intra-observer error. Separate standards were utilized for the upper central incisors, the upper lateral antimeres and the lower teeth. These were later confirmed by G.H. Sperber (Faculty of Dentistry) to be approximately correct.

Hrdlička's fourth-degree system was followed, except that barrel-form elements were added to the scale; peglike incisors were considered to be nonshovel-shaped teeth.

Two samples of 15 to 20 individuals were rated by Sperber on two different occasions (May 2/1985 and May 7/1985), so that shovel-grading by Sperber and Tait could be compared. The differences in judgment between Sperber and Tait amounted to half a grade at the most (e.g., trace + vs. semi -), and were confined to the semishovel and trace-shovel categories in the upper teeth. There were no discrepancies in the scoring of mandibular incisor shovelling.

In regard to labial ridging, the procedure followed was basically that of Kirveskari (1974) and K.E. Wright (1977:15). Mesial and distal facial ridges were scored as "present" when they were distinctly more prominent than the central lobe, so that the difference was appreciable to the naked eye. Weak labial ridges were placed in the "absent" category.

3.3.7 Observations on shovelling trait.

Observations for the Grimsby specimens are given in Tables 2a - 4b (pp. 71-76). The maxillary incisors usually displayed the full-shovel grade, the frequently being greater for the central incisors (26/32; 81.3%) than for the lateral antimeres (15/40; 37.5%). The difference between

TABLE 2a. LINGUAL SHOVELLING OF MAXILLARY INCISORS IN THE GRIMSBY SAMPLE: OCCURRENCE BY SIDE.

	CENTRAL INCISOR		LATERAL INCISOR	
	L SIDE	R SIDE	L SIDE	R SIDE
SEX	#	#	#	#
MALE				
none	0	0	1	1
trace	1	2	2	3
semi	0	0	3	4
full+	13	12	7	8
deep	3	3	0	2
barrel	0	0	2	0
total	14	14	15	16
asymmetry				
FEMALE				
none	0	0	1	0
trace	0	0	4	4
semi	2	2	4	3
full+	5	10	7	6
deep	3	3	1	1
barrel	0	0	1	0
total	7	12	17	13
asymmetry				
ALL				
none	0	0	2	1
trace	1	2	8	9
semi	4	4	9	9
full+	20	24	14	14
deep	8	8	1	3
barrel	0	0	3	0
total	25	30	36	33
asymmetry				

+ Category includes all deep-shovel grade specimens.

TABLE 2b. LINGUAL SHOVELLING OF MAXILLARY INCISORS IN THE GRIMSBY SAMPLE: OCCURRENCE BY INDIVIDUAL

SEX	CENTRAL INCISOR INDIVIDUAL # (%)	LATERAL INCISOR INDIVIDUAL # (%)
MALE		
none	0 (0.0)	1 (5.6)
trace	2 (13.3)	3 (16.7)
semi	0 (0.0)	4 (22.2)
full+	13 (86.7)	8 (44.4)
deep	3 (20.0)	1 (5.6)
barrel	0 (0.0)	2 (11.1)
total	15 (100)	18 (100)
asymmetry	0/15	
FEMALE		
none	0 (0.0)	1 (5.6)
trace	0 (0.0)	5 (27.8)
semi	2 (16.7)	4 (22.2)
full+	10 (83.3)	7 (38.9)
deep	3 (25.0)	1 (5.6)
barrel	0 (0.0)	1 (5.6)
total	12 (100)	18 (100)
asymmetry	0/12	
ALL		
none	0 (0.0)	2 (5.0)
trace	2 (6.3)	10 (25.0)
semi	4 (12.5)	10 (25.0)
full+	26 (81.3)	15 (37.5)
deep	9 (28.1)	2 (5.0)
barrel	0 (0.0)	3 (7.5)
total	32 (100)	40 (100)
asymmetry	0/32	

+ Category includes all deep-shovel grade specimens.

TABLE 3a. LABIAL SHOVELLING OF MAXILLARY INCISORS IN THE GRIMSBY SAMPLE: OCCURRENCE BY SIDE.

	CENTRAL INCISOR		LATERAL INCISOR	
SEX	L SIDE #	R SIDE #	L SIDE #	R SIDE #
MALE				
mesial	2	2	2	1
total	13	12	14	14
distal	0	1	0	0
total	10	11	16	13
FEMALE				
mesial	1	2	1	1
total	10	11	16	13
distal	0	2	0	1
total	11	11	19	17
ALL				
mesial	4	5	5	3
total	28	27	34	31
distal	0	3	0	1
total	30	27	39	36

TABLE 3b. LABIAL SHOVELLING OF MANDIBULAR INCISORS IN THE GRIMSBY SAMPLE: OCCURRENCE BY INDIVIDUAL.

SEX	CENTRAL INCISOR INDIVIDUAL # (%)	LATERAL INCISOR INDIVIDUAL # (%)
MALE		
mesial	2 (14.3)	2 (11.8)
total	14 (100)	17 (100)
distal	0 (6.7)	0 (0.0)
total	13 (100)	19 (100)
FEMALE		
mesial	2 (15.4)	2 (10.5)
total	13 (100)	19 (100)
distal	2 (15.4)	1 (4.5)
total	13 (100)	22 (100)
ALL		
mesial	6 (18.2)	6 (15.0)
total	33 (100)	40 (100)
distal	3 (9.1)	1 (2.2)
total	33 (100)	45 (100)

TABLE 4a. LINGUAL SHOVELLING OF MANDIBULAR INCISORS IN THE GRIMSBY SAMPLE: OCCURRENCE BY SIDE.

	CENTRAL INCISOR		LATERAL INCISOR	
SEX	L SIDE \#	R SIDE \#	L SIDE \#	R SIDE \#
MALE				
none	9	7	7	11
trace	2	2	4	1
semi	1	1	1	1
total asymmetry	12	10	12	13
FEMALE				
none	4	6	8	5
trace	8	6	9	10
semi	1	0	2	2
total asymmetry	13	12	19	17
ALL				
none	17	17	17	16
trace	12	10	16	15
semi	4	3	4	4
total asymmetry	33	30	37	35

*Specimen with trace/semi-grade asymmetry present; others have absent/trace grade asymmetry.

TABLE 4b. LINGUAL SHOVELLING OF MANDIBULAR INCISORS IN THE GRIMSBY SAMPLE: OCCURRENCE BY INDIVIDUAL.

SEX	CENTRAL INCISOR INDIVIDUAL # (%)	LATERAL INCISOR INDIVIDUAL # (%)
MALE		
none	9 (75.0)	10 (66.7)
trace	2 (16.7)	4 (26.7)
semi	1 (8.3)	1 (6.7)
total	12 (100)	15 (100)
asymmetry		
FEMALE		
none	5 (35.7)	6 (30.0)
trace	8 (57.1)	11 (55.0)
semi	1 (7.1)	3 (15.0)
total	14 (100)	20 (100)
asymmetry		
ALL		
none	19 (54.3)	18 (42.9)
trace	12 (34.3)	19 (45.2)
semi	4 (11.4)	5 (11.9)
total	35 (100)	42 (100)
asymmetry		

*Specimen with trace/semi grade asymmetry present; others have absent/trace grade asymmetry.

the incidences for these two teeth was found to be highly significant ($X^2p = 0.000$). The lateral incisor percentage did not include three individuals (7.5%) which had strongly shovel-shaped laterals on one side and barrel-shaped antimeres on the other. Barrel-form teeth only occurred on the left side of the upper jaw. Moderate shovelling was observed in 12.5% of the central incisors and 25.0% of the lateral incisors, while ridge traces were found in 6.3% and 25.0%, respectively, of these teeth.

Lingual ridging was slightly stronger in male specimens than female ones. Males had marked shovelling on 86.7% of the central incisors (13/15) and 44.4% of the lateral incisors (8/18). The incidence for females was not significantly different (10/12; 83.3% and 7/18; 38.9%).

Shovelling was much less robust in the mandibular incisors. Moderately shovel-shaped central incisors occurred in 11.4% (4/35) of the Grimsby individuals, and moderately shovel-shaped laterals in 11.9% (5/42). The teeth of the remaining individuals were classified as trace (34.3% for the I^1; 45.2% for the I^2) or nonshovel (54.3% for the I^1; 42.9% for the I^2).

The incidences of moderate shovelling in the mandibular incisors of males and females were similar. Sexual differences were evident in the frequencies of the trace and absent categories, but the distinction between these two classes is rather subtle. Therefore, discrepancies between the recorded proportions are unlikely to be significant.

Lateral grade asymmetry for the shovel-shape feature was absent in the maxillary central incisors, but present in 7.5% (3/40) of the upper lateral antimeres. The pattern was similar for the mandibular incisors, with asymmetry present in 2.9% (1/35) of the central teeth and 9.5% (4/42) of the lateral teeth.

Prominent labial ridges were observed on both central and lateral incisors (see Table #4, p. 59). Mesially-ridged central teeth were displayed by 18.2% (6/33) of the Grimsby specimens while distally-ridged central teeth were found in only 9.1% (3/33). A total of eight individuals manifested facial ridges of some kind, including one instance of a double-shovel (Fe9 #26, RI[1]). Labial ridges were much weaker on the lateral incisors but occurred almost as frequently (manifested on seven individuals). Mesially-ridged lateral teeth were displayed by 15.0% (6/40) of the Grimsby specimens while distally-ridged lateral teeth were found in a mere 2.2% (1/45). Distofacial ridges on both central and lateral incisors were observed only on the right side of the upper jaw.

Only very slight labial ridges occurred on the mandibular incisors. In three specific cases, this ridging was noticeably stronger than in other individuals, and might be referred to as very weak mesial three-quarter shovelling facial ridges were not distinctly more prominent than the central lobe in any of these specimens.

3.4 Lingual tubercles and other cingular features of maxillary incisors.

3.4.1 Various aspects of lingual tubercles and other cingular features.

The lingual tubercle or cusp (see Figure 8a, p. 80) is a rounded protuberance partially separated from the rest of the basal cingulum (and the lingual fossa) of the incisor (or canine) by a distinct groove, furrow or gap (Barnes, 1969; Scott, 1973:27). It is usually a small nodule or "bud" rather than a cusp; however, in a very few cases it takes the form of a large talon eminence that can reach the incisal edge of the crown (Hrdlicka, 1921; Pedersen, 1949:Plate. 30; Woelfel, 1984:233, 235). Tubercles may be single or paired; the apex may be fused, partly or completely free, and simple or divided in form (Hrdlicka, 1921; Turner, 1967b:37).

The lingual tubercle has often been associated with a number of other accessory features arising from the cingulum of the anterior teeth (see Figures 7b,7c, pp. 81-82). These include "fingerlike" medial enamel ridges which extend well into the lingual fossa, and much smaller enamel extensions or elevations ("welts", "cingular bridges" or "cingular spurs"), which are not clearly separated off from the cingulum. The cingulum or "basal heel" may also vary

Figure 8a. Cingular features of maxillary incisors: lingual tubercles.

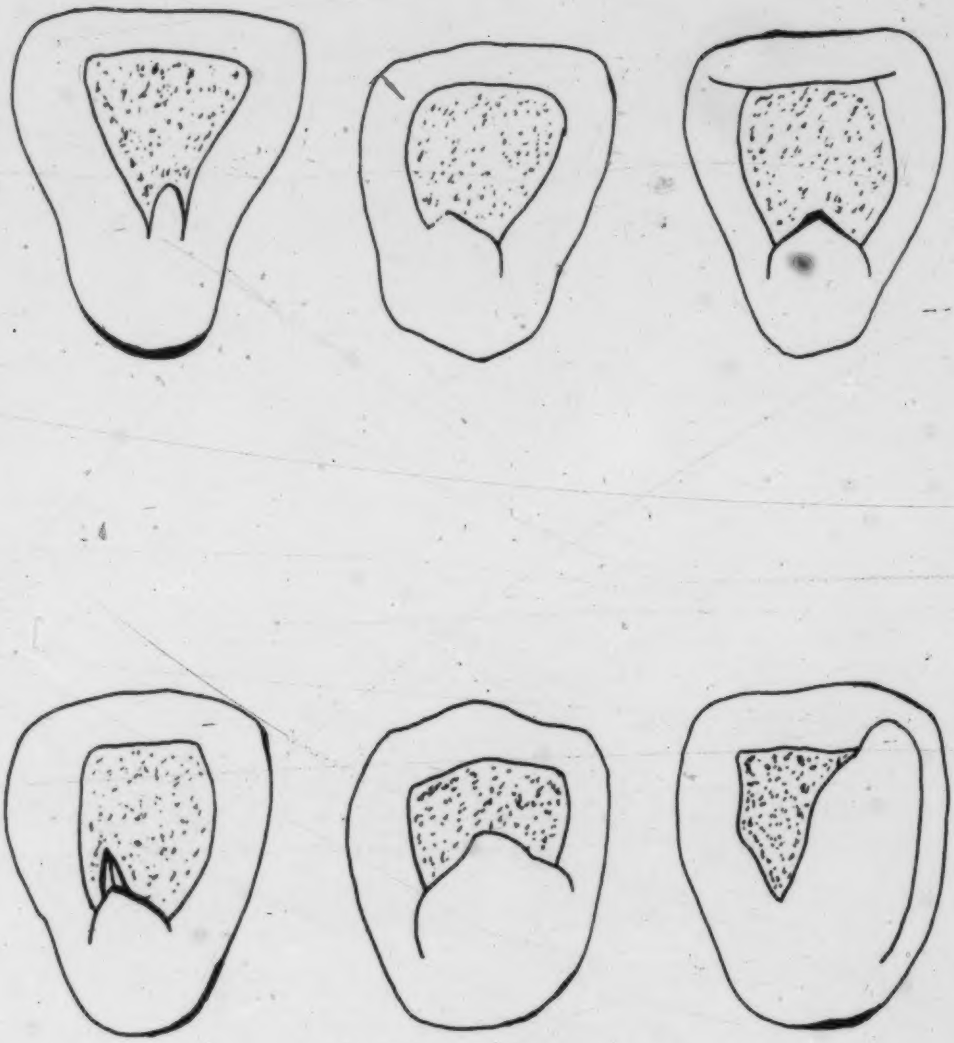


Figure 8b. Cingular features of maxillary incisors: medial lingual ridges.

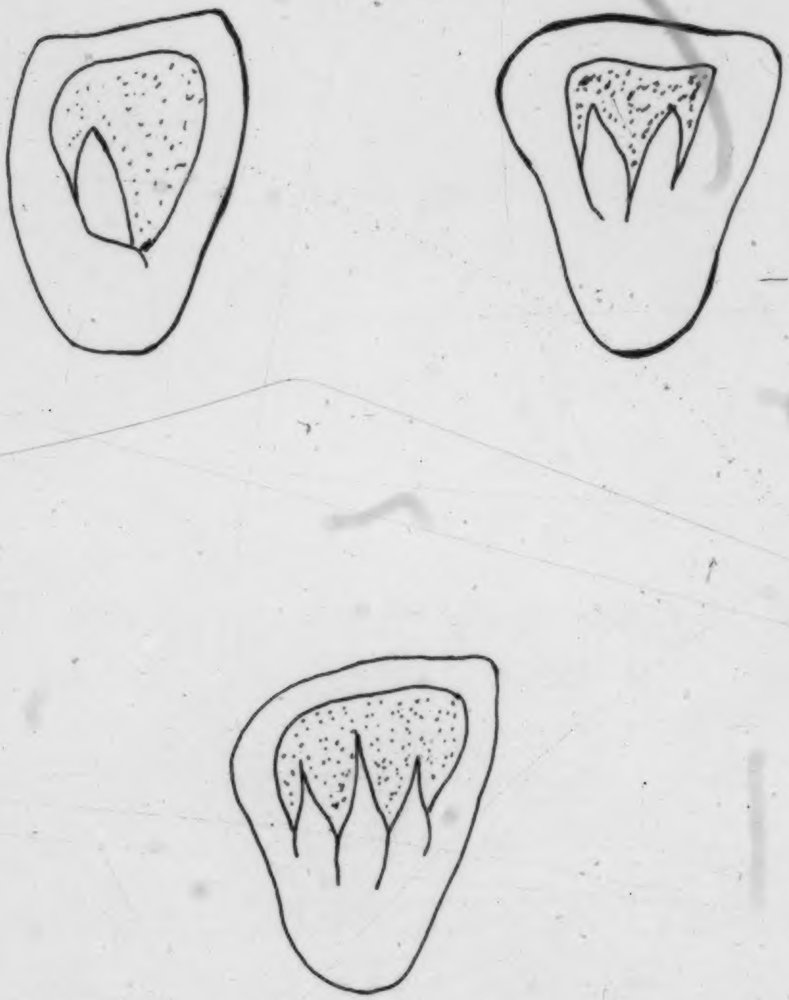
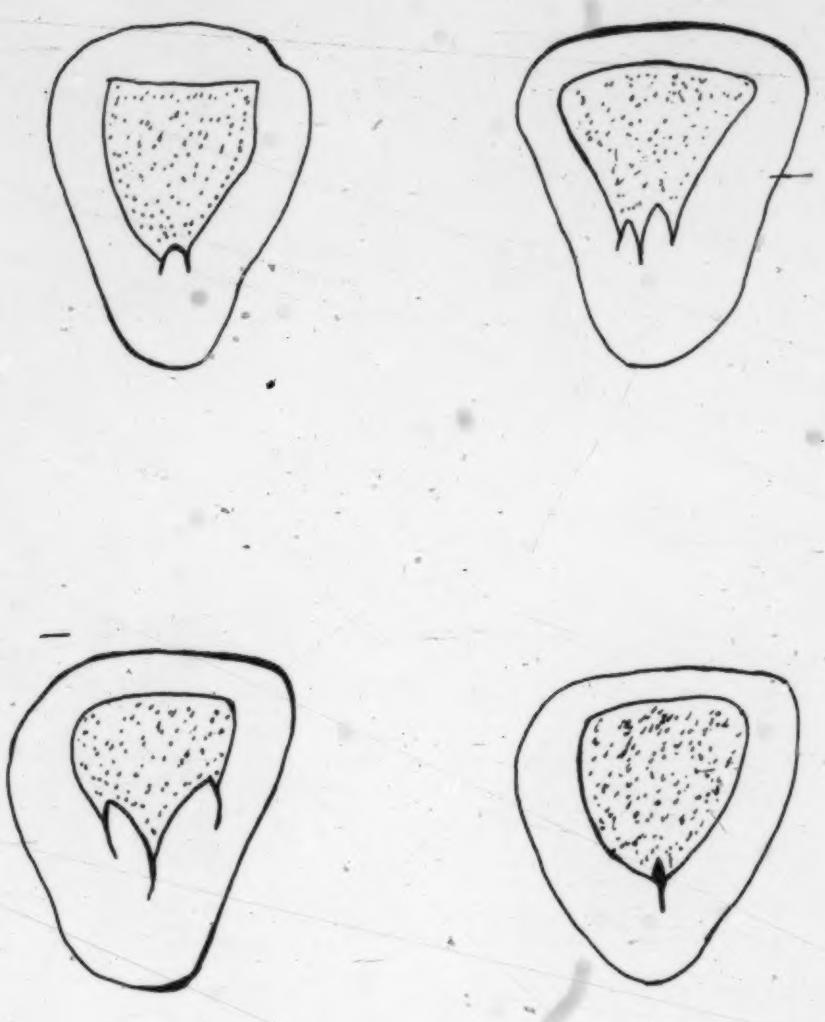


Figure 8c. Cingular features of maxillary incisors: spurs and pits.



greatly in its form and degree of development; it can be lacking or inconspicuous; it may be represented merely by a "thickening" between the marginal ridges or replaced by a fusion or extension of these ridges. Cingular development can vary from a very slight swelling to a moderate convexity to a pronounced tuberosity (Hrdlička, 1920; 1921; Weidenreich, 1937a:18-21). The cingulum may also be marked by "notches" or pits at its incisal edge (Barnes, 1969).

Unfortunately, the lingual tubercle has usually not been clearly distinguished from other cingular features. Black (1897:xvii), Hrdlička (1921) and Diamond (1929:46; 1952:86) defined the lingual tubercle or cusp as a prominent, rounded single or double eminence protruding from the cingulum of an incisor or canine. This definition does not clearly separate the lingual tubercle from the shorter medial ridge variations or from cingular "spurs" or "welts". Pedersen (1949:179) referred to the lingual cusp as a large "more or less free" eminence, but said nothing specific about smaller tubercles. Morris' (1965:27) description of a lingual tubercle as an elevation with a "palpable tip" is even less useful.

The introduction of the European term "tuberculum dentale" ("dental tubercle" or "tuberosity") into the English literature has only served to further confuse the situation in regard to lingual tubercles and associated features. De Jonge-Cohen (1926) and Weidenreich (1937a:16-

21) included a number of cingular manifestations under this expression, including medial enamel ridges, pronounced tuberosities and lingual cusps. Pedersen (1949:186-188) limited the term to variations of the linguocervical region, including tubercles and cusps, and excluded median ridges. Neither Lasker (1950) nor Carbonell (1963) defined what was included in the "dental tubercle". Turner (1967b:39) restricted the expression to the lingual cusp manifestation; i.e., a marked eminence having a "free or only weakly attached apex". Scott (1973:25-26) included accessory features (e.g., medial ridges, cingular bridges lingual cusps) in his "tuberculum dentale" category but did not describe degree of tuberosity development.

Research on lingual tubercles and other cingular manifestations has usually been done on the maxillary incisors. Hrdlička (1921) was the first to give "lingual cusps" frequencies for various racial groups. He found that there were no marked discrepancies between Euro-Americans, Afro-Americans and Amerindian samples, in which the tubercle incidence ranged from ca. 2.5% - 3.0% for the central teeth and ca. 7.5% - 9.0% for the lateral antimeres. Carbonell (1963) presented statistics for "dental tubercle" frequencies on the lateral elements for 11 different (mainly Old World) populations, which indicated that most racial groups have low proportions of tuberculated incisors (ca. 1% - 5%). This result is in general agreement with Hrdlicka's findings, although figures from the two authors are not strictly comparable.

However, there is good evidence that some modern populations have much higher incidences of the lingual cusp than those usually reported, e.g., by Hrdlička (1921) and Carbonell (1963). The latter found three exceptional samples with values of ca. 20%: East Greenland Eskimos and two Middle Eastern groups (Palestinians, Mesopotamians). Scott (1973:161-167) found low to moderate frequencies (15% - 30%) of lingual tubercles on the lateral incisors of his southwestern Amerindian, Euro-American and Easter Island populations. The marked discrepancies between his figures for these groups and those of other worker for similar groups emphasizes the importance of establishing a standard set of criteria for the evaluation of anatomical features.

Maxillary incisors display one lingual tubercle much more commonly than two (Hrdlicka, 1920; Turner, 1967b:45; Scott, 1973:164-167), and very rarely, three may be manifested (Pedersen, 1949:pl. #27; Kraus et al., 1969:19; Woelfel, 1984:233). Lateral antimeres invariably have a much higher frequency of tubercles (ca. 3.0 - 6.0 times greater) than the central elements (Hrdlička, 1920; Pedersen, 1949:187; Turner, 1967b:45). In many populations, the latter (I^1) may lack definite tubercles, while the former (I^2) may have significant incidences (ca. 10% - 35%) of the feature, e.g., Aleuts, Athapascans, Southwestern

Amerindians, Euro-Americans, Easter Islanders and Griquas (Turner, 1967b:45; Scott, 1973:161-167; Kieser, 1984a). Generally, lingual tubercles are much more likely to be bilaterally rather than unilaterally expressed (Hrdlička, 1921).

Lingual tubercles and associated features do not seem to be sexually dimorphic. Hrdlička (1921) found that male and female incidences for "lingual cusps" were not markedly different. Carbonell (1963) did not test her figures for sexual differences. Turner (1967b:39) found no significant dimorphism in his pooled Arctic samples and Barnes (1969) found none in his Ugandan Teso groups. Scott (1973:161-167) tested seven Southwestern Amerindian tribes and two Euro-American populations, but did not find evidence of significant male-female differences in tuberculated incisor frequencies; neither did Turner (1979) for his Japanese Jomon or Kieser (1984a) for his South African Griqua dentitions.

Mandibular incisors display only single lingual tubercles and only rarely manifest these features, in all populations so far studied. These groups include: Euro-Americans, Orientals, East Greenland Eskimos, Southwestern Amerindians (Hrdlicka, 1921; Weidenreich, 1937a:24; Pedersen, 1949:181; Morris, 1965:265). Scott (1977b) has remarked that lingual tubercles are not found in the lower canine, which indicates the low frequency of this character on the anterior teeth in general.

In recent research, there is a tendency to associate lingual tubercles and welts with medial enamel ridges, as related cingular manifestations (Barnes, 1969; Scott, 1973:25-26). Hrdlička (1921) and Turner (1967b:44, 48) have noted that the two features are probably related, as tubercles occasionally have a "ridgelike" form, but both authors examined them separately in their initial publications. Turner (1979; 1983; 1985; 1987) has recently included medial ridges in the "tuberculum dentale" complex. However, none of the modern workers has considered the different degrees of development of the "basal heel" in their morphological and statistical studies on the linguocervical region of anterior teeth, although it seems very likely that the character is part of the same "polymorphic" continuum as lingual tubercles, cingular bridges and median ridges (Hrdlička, 1921; Weidenreich, 1937a:16-21).

Medial lingual ridges are enamel elevations which are located between the two marginal crests (see Figure 8b, p. 81), they extend from the cingulum towards the incisal edge for varying distances (Hrdlička, 1921; Turner, 1967b:44). Hrdlička (1921) noted that up to three medial ridges might be found on the upper incisor, but that a single central one was most likely to occur, and three ridges were only rarely manifested. Turner (1967b:47, 50) and Scott (1973:161-167) have recently confirmed these observations in their statistical studies; the single-ridge form was determined to be the most common overall and the three-ridge type was virtually absent on the lateral incisors and only rarely displayed by the central antimeres (ca. 0% - 5%, except for the Easter Island population, given as ca. 10%).

Medial ridging occurs much more commonly on the central incisors than the lateral ones. Eskimo populations display frequencies of ca. 80% on the central teeth and ca. 70% on the lateral antimeres; Aleuts (pooled samples) show ca. 70% and ca. 60%, respectively (Turner, 1967a:47, 50). In seven Southwestern tribes, the incidence of medial ridging varied from ca. 55% - 90% in the upper central incisors and from ca. 15% - 35% in the upper lateral teeth. For two Euro-American populations the figures were ca. 65% and ca. 25%, respectively, and for the Easter Island dentitions, they were 90% and 40%, respectively (Scott, 1973:161-167).

The frequencies of single and double medial-ridging show different patterns for the two upper incisors. Most racial groups examined so far display approximately equal incidences of single and double-ridged central incisors, ca. 20% - 35%, e.g., Aleuts (pooled samples), Southwestern tribes, Euro-Americans (Turner, 1967b:50; Scott, 1973:161-167). In a couple of cases (Eskimos, Easter Islanders) the double-ridged form (50% - 60%) is much more common than the single-ridged type (20% - 30%).

In the lateral antimeres, however, the single-ridged form occurs much more often, (15% - 30%) than the double-ridged type (2% - 10%). Arctic populations are exceptional in this regard (Turner, 1967b:50; Scott, 1973:161-167). In Eskimo groups, single-ridged incisors are predominant but by a lesser margin than is usually found (ca. 40% to ca. 30%), while Aleut (pooled) samples more frequently display double-ridged teeth (ca. 40% to ca. 25%).

In general, marked sexual dimorphism does not seem to occur for the medial lingual ridge character. Barnes (1969) found a significant sexual differences ($\overline{x^2}p<0.01$) for the upper central incisors of his Ugandan Teso group, with the feature predominating in females. Turner (1967b:47) tested his pooled Arctic samples and could not demonstrate significant dimorphism, but noted that females had slightly higher values than males. Scott (1973:161-167) did not observe significant discrepancies in male-female incidences of medial ridging for any of the 12 populations considered in his thesis.

Medial lingual ridges are much less common and robust on the mandibular incisors (Hrdlička, 1921; Turner, 1967b:44, 47). Double medial-ridging is found only rarely (0% - 4%) on the lower teeth and total medial-ridging is generally well under 50%. Medial enamel ridges seem to be much more common on the lateral incisors (48%) than the central ones (14%) in Arctic populations (Turner, 1967b:47).

Lingual tubercles, medial ridges and related cingular features may function as structural supports for the anterior dental elements. Hrdlička (1921) thought that medial ridges strengthened the lobes of the front teeth. Weidenreich (1937a:18-19, 26) believed that lingual tubercles and dental tuberosities acted as "buttresses" which reinforced the incisor (or canine) against side to side grinding or cutting pressures, and that cingulotubercular bulk became reduced in the course of human evolution as these forces declined in strength.

Turner (1967b:42-~~43~~, 48) remarked that medial ridges and tubercles may function to strength the incisors of populations with harsh dietary regimens. He found that tubercles contribute significantly to the total coronal mass, thereby increasing the utility span of the tooth. The feature might also serve to protect the upper anterior gingival tissue by retarding the vertical movement of the lower incisors, in cases where the molar cusps are too badly worn to serve this purpose.

These functions would be particularly important in High Arctic groups (e.g. Eskimos) where dental attrition was rapid and severe (Turner, 1967b:43, 48; 1985). It is noteworthy that Eskimos have some of the highest recorded frequencies for tuberculated upper incisors (8% for I^1, 47%

for I^2) and double medially-ridged antimeres (ca. 60% for I^1; ca. 30% for I^2). Aleut populations also have relatively high frequencies for these two features (Turner, 1967b:45, 50).

3.4.2 Methodology for lingual tubercles and other cingular features.

Lingual tubercles can be classified according to Scott's (1973:26-27) eight-grade scale, but in the absence of these plaster plaques, tubercles were simply marked as "present" or "absent". Cingular spurs, "notches" and pits were also recorded if observed. No attempt was made to judge the different degrees of "basal heel" development; this would be a very subjective exercise, in which a large intra-observer error would be expected. As Pedersen (1949:187), has remarked, it is impossible in many instances to differentiate a very slight tuberosity from the basal confluence of the usually robust lingual marginal ridges.

Medial lingual ridges are difficult to score because of their very low relief. Pedersen (1949:188) stated that it was not possible to give accurate frequencies for European and Eskimo populations, because many incisors displayed only weak traces of the enamel ridges. Turner (1967b:47) remarked that medial ridges in Arctic dentitions were subjected to early and severe wear by overbiting, resulting in the obliteration or near-obliteration of these structures. Therefore, he could use only a small portion of his sample (viz. juveniles and young adults with slight attrition) for counting medial lingual ridges.

In consideration of the problems noted above, it is apparent that a high interobserver error might occur in scoring medial lingual enamel ridges. For instance, Moorrees (1957:26) stated that medial ridges were rare in living Aleuts while Turner (1967b:50) found them quite common in skeletal Aleuts. In this study, only distinct ridges separated by grooves or furrows were recorded, on a present or absent basis, following K.E. Wright's (1977:12 - 13) procedure. This method gives a conservative value for medial-ridging frequencies; Wright's' (1977:34, 40) figures are rather low compared to those presented by other workers (7.2% for the I^1; 0% for the other anterior teeth). P.J. Wright's (1977:72-73, 82-83) observations were not comparable, as he separated medial ridges from cingular incisal prolongations.

3.4.3 Observations on lingual tubercles and other cingular features.

The observations are given in Tables 5a,5b, (p. 93-94). There was only a single (unilateral) case of a tuberculated central incisor in the Grimsby sample (2.3%, n=43), and the eminence resembled an enlarged, prominent cingular spur rather than a typical tubercle, as defined above. The opposing antimere displayed a cingular spur. These spurs were usually (4/5) unilateral and occurred half as

TABLE 5a. CINGULAR FEATURES ON MAXILLARY INCISORS IN THE GRIMSBY SAMPLE: OCCURRENCE BY SIDE.

	CENTRAL INCISOR			LATERAL INCISOR	
SEX	L SIDE \#	R SIDE \#		L SIDE \#	R SIDE \#
MALE					
tubercles	0	1		1	1
total	18	17		18	17
spur/rdge.	7	5		3	3
notches	1	2		5	6
pits	0	0		0	0
trace					
FEMALES					
tubercles	0	0	1	21	
total	13	17		19	17
spur/rdg.	3	2		1	1
notches	1	0		7	6
pits	0	0		1	1
ALL					
tubercles	0	1		4	4
total	35	37		41	38
spur/rdg.	13	10		7	6
notches	2	2		13	13
pits	0	0		1	1

TABLE 5b. CINGULAR FEATURES ON MAXILLARY INCISORS IN THE GRIMSBY SAMPLE: OCCURRENCE BY INDIVIDUAL.

	CENTRAL INCISOR	LATERAL INCISOR
SEX	INDIVIDUAL # (%)	INDIVIDUAL # (%)
MALE		
tubercles	1 (5.3)	2 (9.5)
total	19 (100)	21 (100)
asymmetry	1/1	1/2
spur/rdg.	8 (42.1)	6 (28.6)
notches	2 (10.5)	8 (38.1)
pits	0 (0.0)	0 (0.0)
FEMALE		
tubercles	0 (0.0)	2 (9.5)
total	18 (100)	21 (100)
asymmetry	0/0	1/2
spur/rdg.	3 (16.7)	2 (9.5)
notches	1 (5.6)	9 (42.9)
pits	0 (0.0)	1 (4.8)
ALL		
tubercles	1 (2.3)	6 (13.0)
total	43 (100)	46 (100)
asymmetry	1/1	3/6
spur/rdg.	15 (34.9)	11 (23.9)
notches	3 (7.0)	18 (39.1)
pits	0 (0.0)	1 (2.2)

frequently (11.6%) as medial enamel ridges (23.3%), which were usually (7/10) bilateral. Double medial-ridging was observed somewhat more often than single-ridging. No discernible sexual dimorphism was evident for any of the cingular features on the central incisor.

Lingual tubercles occurred much more commonly on the lateral incisor (13.0%, n=46). However, they were often manifested unilaterally (at least 3/6, with one specimen determinable only for a single side). It is notable that of the three unilaterally-tuberculated specimens, two had either a strong cingular spur or marked medial ridge on the opposing antimere. As a rule, tubercles were easily distinguished from these other features.

Cingular spurs and medial enamel ridges were less frequently found on the lateral incisor than on the central one, with incidences of 10.9% and 13.0%, respectively (n=46). spurs lacked the bulging form of tubercles and were usually (4/5) unilaterally displayed. Medial lingual ridges tended to be unilaterally exhibited (5/6); double medial-ridging was observed at least as often as single-ridging. It was sometimes difficult to determine whether the manifestation was a spur or a medial ridge. There was no discernible sexual dimorphism evident for any cingular features on the lateral incisor.

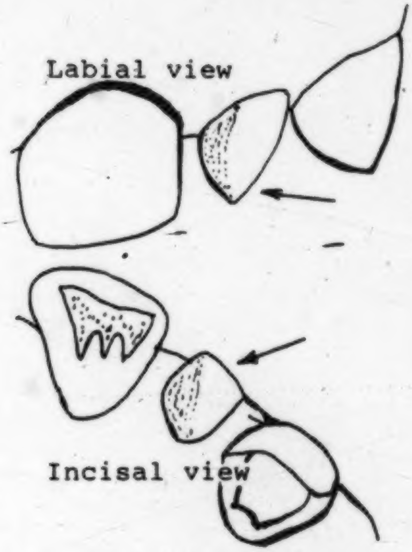
Lingual tubercles were not observed on any of the lower incisors, and neither were cingular spurs nor marked medial ridges. The cingulum of the anterior mandibular elements was nearly always weakly developed. Cingular manifestations do not seem to be particularly useful as diagnostic traits for these teeth.

3.5 Miscellaneous morphological features of maxillary incisors.

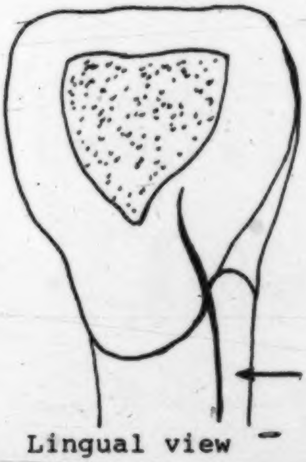
3.5.1 Various aspects of linguocervical grooves and labial shape.

Linguocervical grooves occur on the cingulum and basal root portion of maxillary incisors (see Figure 9, p. 97). They have been called a variety of different names in the past: linguogingival fissures or sulci (Black, 1890:24-28; 1897:26-30; Hrdlička, 1920; Zeisz and Nuckolls, 1949:44, 63), lingual developmental or segmental grooves (Diamond, 1929:45-46; 1952:85; Wheeler, 1940:131, 140, 143; 1974:146-149, 154), lingual marginal grooves (Kraus et al., 1969:21-22), interruption grooves (Turner, 1967b:231-234; 1979; 1983), coronal-radicular grooves (Brabant, 1971) and palatal-gingival grooves (Woelfel, 1984:292). A groove may cut the cingulum near its centre, or, much more frequently, it will cut either the mesial or distal marginal ridges (rarely both) and extend into the cementum of the root (Black, 1890:28; 1897:30; Hrdlička, 1920). Linguocervical grooves are very infrequently observed on the mandibular incisors (Black, 1890:31; 1897:33; Wheeler, 1974:157).

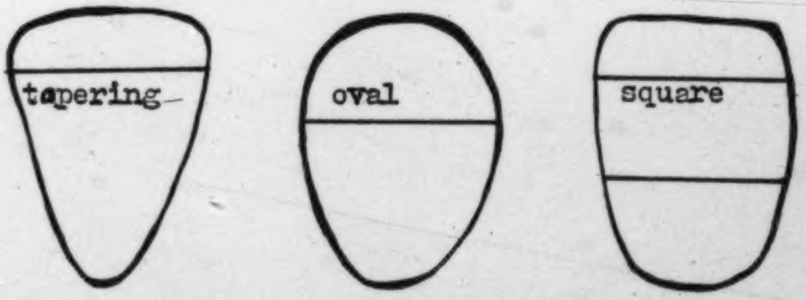
Figure 9. Miscellaneous morphological features of maxillary incisors.


Labial view
Incisal view

Peg-shaped lateral incisor. (Adapted from Woelfel, 1984: 227, Figure 12.1.)


Lingual view

Distal linguocervical groove.


tapering
oval
square

Labial shape. (Adapted from Williams, 1914.)

Mesial and distal linguocervical grooves mark the junction of the spatuate, trilobed portion of the incisor with the basal cingulum, which forms at a later stage in the development of the anterior tooth (Black, 1890:24; 1897:26; Hrdlička, 1920; 1921). During the calcification of the incisor, both grooves can be obliterated, or one may remain as a distinct feature, while the other is very faint or imperceptible. Both grooves are seldom manifested on the same tooth (Hrdlička, 1920). Several workers (Diamond, 1929:46; 1952:85; Wheeler, 1940:140, 143; 1974:148-149; Turner, 1979) have noted that the distolingual groove is more common than the mesiolingual type, while the mediolingual variation is rare.

The limited research done on linguocervical grooves indicates that these impressions are manifested much more frequently on the lateral incisors. Hrdlička (1920) was perhaps the first to observe this fact, and recent statistical studies have supported it. According to Brabant's (1971) table, the grooves occur two to four times more commonly on the lateral incisors of his prehistoric French, Swiss and Belgian populations. Turner's (1979) data indicate that the lateral incisor groove-incidence was four times greater than the central incisor groove-incidence for his Jomon sample.

Only a few studies have given statistics on the occurrence of linguocervical grooves. Brabant (1971) found frequencies in his west European Neolithic and Megalithic dentitions to be ca. 2% - 7% for the central incisor and ca. 6% - 14% for the lateral element. Turner (1979) found that the Japanese Jomon had groove-incidences of 16% for the central incisor and 66% for the lateral one. Linguocervical grooves also occur very commonly in the anterior teeth of Eskimo-Aleut (66% on the I^2), Athapascan (61% on the I^2) and various Amerindian (50% on the I^2) populations (Turner, 1983).

Turner (1979, 1983, 1987) has used lateral incisor frequencies for linguocervical grooves in intergroup comparisons, but other workers (e.g., Scott and Dahlberg, 1982; Scott et al., 1983) have not. Brabant (1971) has remarked that the significance of the feature is not know at the present time. Wheeler (1974:147, 154) considered the character to be an "uncommon variation" or genetic anomaly, as does Sperber (pers. comm., 29/5/1985).

The shape of the facial outline of the central upper incisor was used by Williams (1914; 1928) to categorize the dentition of modern Caucasoids (Europeans) and other racial groups, and even that of the apes. There are three basic types of incisor in his classification: tapering, in which the mesial and distal margins converge towards the cervix or "crown base"; ovoid, in which the mesial margin is more or less straight while the distal is curved outward, in convex fashion; and square, in which the two margins are roughly parallel (see Figure 9, p. 97). Williams also noted the occurrence of a number of combinations of these basic shapes among the populations that were examined.

Diamond (1929:219-220; 1952:176-177) pointed out that Williams did not take into consideration the effects of incisal and interproximal wear in his initial study. These factors could certainly alter the original facial form of an incisor; strong incisal wear might remove the upper one-third of the crown, so that an ovoid outline would be indistinguishable from a square one. However, this problem can be eliminated if the only teeth considered are either unworn or only slightly worn on the incisal surface.

Labial incisor form has not been commonly used as a descriptive trait in the last 40 years, possibly because of the problem of attrition mentioned by Diamond (1929; 1952) and the high probability that this variation has a very complex genetic background. Taylor (1978:344-345, 350) has recently stated that these facial-shape categories are of value in the description of maxillary central incisors, and Kraus et al. (1969:16-17) have also used them. A few workers have given frequencies of the feature for African, Caucasian and Oceanic populations (Stewart, 1931; Kietz, 1944; Reisenfeld, 1956). Gregory (1922:314) suggested that labial incisor shape might have some use in racial comparisons, but very little research has been done with this character.

3.5.2 Methodology for lingucervical grooves and labial shape.

K.E. Wright (1977:13-14) recorded the presence of mesial and distal linguocervical grooves on both upper incisors, a procedure followed here. She scored only grooves which extended into the cementum and "could be felt by a fingernail". For the purposes of this study, all distinct coronal-radicular grooves were counted. P.J. Wright (1974:18-23) did not consider this character.

Only central incisors were scored for labial shape (see Figure 5, p. 35), using a classification based on that of Williams (1914) and illustrated by Taylor (1978:345, Figure 10.2). The only teeth considered were those that showed little or no incisal wear. The degree of attrition was judged by the amount of exposed dentine; only specimens with small spots or very narrow "lines" were categorized. The mesial and distal surfaces of the usable antimeres were also carefully examined, to ensure that significant interproximal wear had not occurred. In cases where there was some doubt regarding the shape of the incisor, measurements were taken with a Boley gauge at different heights on the facial surface.

3.5.3 Observations on linguocervical grooves and labial shape.

Linguocervical grooves occurred much commonly on the lateral incisors (57.1%, n=14) than on the central antimeres

(6.7%, n=15). Distal linguocervical grooves occurred twice as frequently as mesial grooves, which appeared more often than the medial type. The groove was manifested bilaterally as often as unilaterally; there was no evidence of marked discrepancies between male and female incidences.

The maxillary central incisors were invariably of the square form, with some tapering tendency in their facial outline (100%, 22/22). No sexual dimorphism was evident, and lateral asymmetry did not occur. Interproximal wear was not a significant factor in the casts chosen for classification.

CHAPTER 4.

MAXILLARY AND MANDIBULAR CANINES.

4.1 Introduction.

This section will focus on two anatomical characters: the lingual tubercle and distal accessory ridge. The former feature is found almost exclusively on the upper cuspid. It was used by Suzuki and Sakai (1966) in their study of a Japanese population from the Chubu district. Kirveskari (1974:15-21, 26-28) determined the incidence of the canine "tuberculum dentale" trait for his three Skolt Lapp groups. Turner (1979) and Kieser (1984a) have recently examined this character in Jomon and Griqua dentitions. Scott (1971, 1973:167-169) has found that tuberculated (upper) canine proportions are particularly useful in interdemic comparisons.

The second trait considered in detail here is the lingual distal accessory ridge, exhibited by both upper and lower cuspids. This was used by Morris (1965:244-282) in his study of Papago-Pecos Pueblo relationships. However, Scott (1973:169-174; 1977a) was the first to thoroughly investigate the importance of distal ridge frequencies as diagnostic characters for comparing different populations, e.g. Southwestern tribes, Athapascans, Euro-Americans. Turner (1985) has found the trait useful for differentiating Mongoloid and non-Mongoloid groups.

Another dental attribute sometimes used in the description of canine anatomy is the shovelling trait. Lingual marginal ridging occurs on both upper and lower cuspids, although the presence of a distinct medial ridge tends to obliterate the lingual fossa. However, the shovel-shape character will be considered in a miscellaneous morphological features subsection at the end of the chapter.

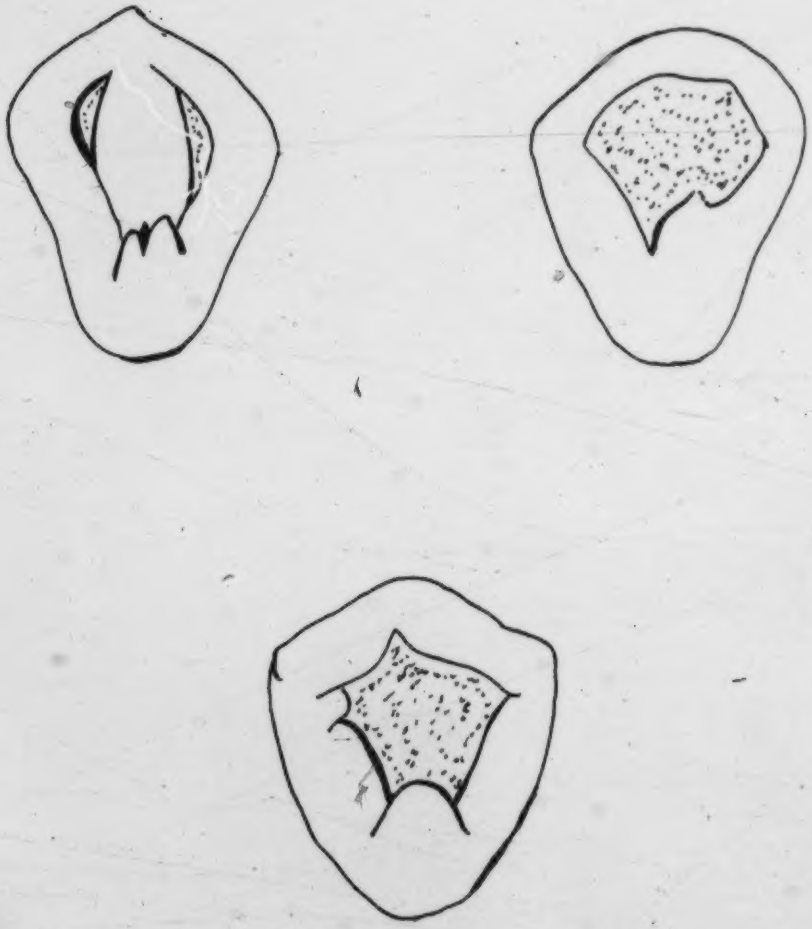
It might also be noted that some of these traits are of phylogenetic importance. Scott (1977b) has observed cingular ridges on the canines of Ramapithecus. Weidenreich (1937a:27-30, b:Plate 5) noted the occurrence of tubercles and shovelling on the upper cuspids of the Choukoutien pithecanthropines. Lingual tubercles and marginal ridging have also been noted on australopithecine specimens from East and South Africa (Robinson, 1956:110; Johanson et al., 1982).

4.2 Lingual tubercles and other cingular features on maxillary and mandibular canines.

4.2.1 Various aspects of lingual tubercles and other cingular features.

Lingual tubercles and associated ridges and "spurs" are found on the upper canines as well as on the upper incisors (see Figure 10, p. 105); usually only a single cuspule is observed (Black, 1890:10,20,35-36; 1897:7,25,38); Hrdlička, 1921; Turner, 1967b:37,45; Kirveskari, 1974:26-28,83). The feature can vary from a small, distinct "bud" with a groove

Figure 10. Lingual tubercles and cingular features of canines - Grimsby specimens.



on one side to a very large, robust tubercle with a free apex (Scott, 1973:27; Scott and Dahlberg, 1982). In some cases, it has been reported to reach the size of broad talon cusp (Windle and Humphreys, 1887; Pedersen, 1949:174).

Only rough comparisons between figures presented by different workers can be made because of the variable definitions used for this character. The term "lingual tubercle" is defined here in the same way as it was for the incisors, i.e. as a distinct, rounded, basal prominence partially separated off from the rest of the cingulum by a distinct groove, furrow or gap (Barnes, 1969; Scott, 1973:27). Some authors (e.g. Kirveskari, 1974:28; Kieser, 1984a) have included medial lingual ridges and cingular bridges in their lingual tubercle or "tuberculum dentale" complex, while others (e.g. Turner, 1967b:39) have only counted "lingual cusps" with free or nearly free apices.

A number of studies have considered the canine lingual tubercle as a particularly important feature in interdemic comparisons. Morris (1965:33,244-282) compared "tubercumum dentale" frequencies for living Papago and extinct Pecos Pueblo samples. Turner (1967b:45) compared several skeletal Arctic populations (Aleuts, Eskimos, Athapascans), and determined that tuberculated cuspid incidences ranged from ca. 5% (Aleuts) to ca. 20% (Eskimos) and ca. 30% (Athapascans). Kirveskari (1974:27) found that three Skolt Lapp populations had proportions of ca. 50% for the "tuberculum dentale" feature, while marked or multiple expressions ("lingual cusps") averaged ca. 10%. Turner's (1979) statistics yield a figure of ca. 55% for his Jomon dentitions, but he did not give a definition of his "tuberculum dentale" category. According to Kieser's (1984a) study, ca. 20% of Griqua canines showed "trace" or "moderate" degrees of the "tuberculum dentale" trait, but no "lingual cusps" were observed.

Scott (1971; 1973:167-169) found that canine lingual tubercle frequencies ranged from a low of ca. 50% - 60% in Arctic (Eskmo, Aleut) and Asio-Indian groups, to a high of ca. 80% - 90% in African and Oceanic (Yap, Easter Island) populations. He determined that 10 Southwestern samples, representing seven tribes, had proportions of tuberculated cuspids varying from ca. 50% - 90%, with the mode being ca. 70% and the "best range" being 65% - 85%. Most tubercles were small to moderate in size. The two Euro-American populations examined had incidences of 70% - 75% for the feature.

The lingual tubercle is rare or absent on the lower canine, according to studies done so far on a number of populations, e.g. European and American Caucasoids, Orientals, Popago and Pecos Pueblo (Black, 1890:39; 1897:41; Weidenreich, 1937:32,34; Morris, 1965:269). Scott (1977a) has stated that the trait only occurs on the upper eye-teeth in modern man. Other cingular features, e.g. accessory ridges, spurs and pits, are also seldom observed.

The mode of inheritance of the lingual tubercle appears to be autosomal and polygenic. Turner (1967b:39) found that males in his pooled Arctic samples had a slightly lower incidence (by ca. 5%) than females. According to Kieser's (1984a) figures, exactly the opposite was true for his Griqua dentitions. In neither case was the difference statistically significant (at x^2 $p<0.05$ level), and this result holds true for other populations tested for sexual dimorphism, e.g. American Southwest tribes (with a single exception), Skolt Lapps, Jomons, Pimas (Scott, 1973:56-57; Kirveskari, 1974:28; Turner, 1979; Scott et al., 1983).

Scott (1971) initially proposed a codominant, two allele model for the lingual tubercle trait; this was found to fit the data for 14 families studied and also that for 10 of 12 populations tested for concordance. The two weakest classes of his (1971) six-grade scale were considered to be heterozygous in this model. However, Scott has lately changed his opinion on the matter, after further research, and now supports a polygenic mode of inheritance (Scott and Dahlberg, 1982; Scott et al., 1983).

4.2.2 Methodology for lingual tubercles and other cingular features.

Scott's (1973:27) recent eight-grade plaque was not available at the University of Alberta, therefore, a comparable rating of different degrees of canine tuberculation was not possible. Kirveskari (1974:27-28) used a seven-class scale, based on size (small or large) and type (single, double, multiple), but this included medial lingual ridges in the small tubercle category. In this study, K.E. Wright's (1977:12-13) definition of a tubercle was accepted (following Barnes, 1969). Lingual tubercles were intially classified according to size (small or large), apex type (fused or free), and number manifested on a single tooth (single, double, multiple). The occurrence of cingular pits and spurs was also noted, for both upper and lower cuspids.

4.2.3 Observations on lingual tubercles.

Observations are given in Tables 6a,6b (pp. 110-111). The upper canines more commonly displayed lingual tubercles (30.6%, n=36) than the two incisors (I^1 and I^2) of the same jaw. No large talon cusps were found; all manifestations were cuspules constituting only a small fraction of the crown mass. The proportions of tubercles with fused (5/11) and free (6/11) apices were approximately the same. Tubercles tended to be bilateral in their occurrence (at least 54.5% of 11 recorded examples), there being only one definitie unilateral case (9.1%). The incidence of the trait seems to be sex dependent in the Grimsby population ($x^2p=0.007$); the male frequency was much higher (50.0%,

TABLE 6a. LINGUAL TUBERCLE AND CINGULAR FEATURES ON CANINES IN THE GRIMSBY SAMPLE: OCCURRENCE BY SIDE.

SEX	MAXILLARY CANINE L SIDE #	MAXILLARY CANINE R SIDE #	MANDIBULAR CANINE L SIDE #	MANDIBULAR CANINE R SIDE #
MALE				
free apex	3	4	0	0
tubercles+	5	8	0	0
total	14	13	14	14
asymmetry				
spurs	5	5	0	0
pits	3	2	0	0
FEMALE				
free apex	0	0	0	0
tubercles+	1	1	0	0
total	14	12	13	13
asymmetry				
spurs	4	5	0	0
pits	0	2	0	0
ALL				
free apex	4	5	0	0
tubercles+	7	10	0	0
total	31	27	31	31
asymmetry				
spurs	11	12	0	0
pits	4	5	0	0

+ Category includues tubercles with both free and fused apices.

TABLE 6b. LINGUAL TUBERCLE AND CINGULAR FEATURES ON CANINES IN THE GRIMSBY SAMPLE: OCCURRENCE BY INDIVIDUAL.

SEX	MAXILLARY CANINE INDIVIDUAL # (%)	MANDIBULAR CANINE INDIVIDUAL # (%)
MALE		
free apex	5 (27.8)	0 (0.0)
tubercles+	9 (50.0)	0 (0.0)
total	18 (100)	16 (100)
asymmetry	1/9	-
spur/tub.++	2/9	-
spurs	7 (38.9)	0 (0.0)
pits	4 (22.2)	0 (0.0)
FEMALE		
free apex	0 (0.0)	0 (0.0)
tubercles+	1 (6.7)	0 (0.0)
total	15 (100)	15 (100)
asymmetry	0/1	-
spur/tub.++	0/1	-
spurs	7 (46.7)	-
pits	2 (13.3)	0 (0.0)
ALL		
free apex	6 (16.7)	0 (0.0)
tubercles+	11 (30.6)	0 (0.0)
total	36 (100)	36 (100)
asymmetry	1/11	-
spur/tub.++	2/11	-
spurs	14 (38.9)	0 (0.0)
pits	8 (22.2)	0 (0.0)

+ Category includes tubercles with both free and fused apices.

++ Category includes cases where ridges are associated with tubercles either on the same tooth or on the opposing antimere.

n=18) than the female one (6.7%, n=15). Cingular spurs and ridges were also observed on the upper cuspid, but were not seen on the lower one.

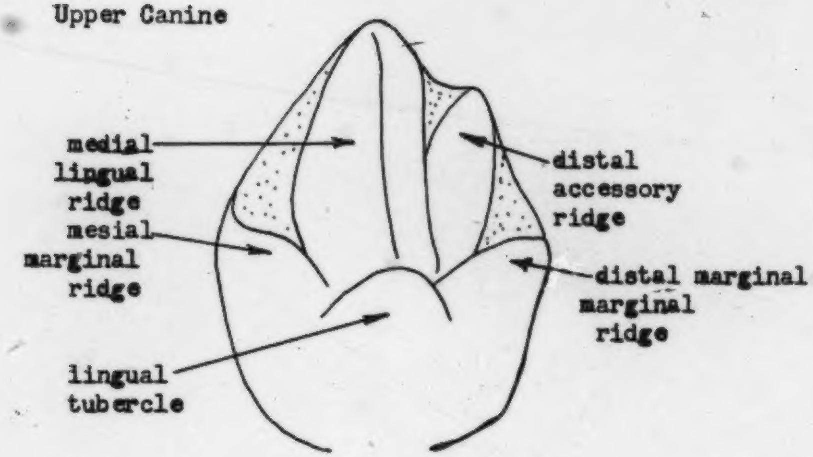
4.3 Distal accessory ridge of maxillary and mandibular canines.

4.3.1 Various aspects of the distal accessory ridge.

Weidenreich (1937:28) noted the presence of a distomedial lingual ridge on the human maxillary canine several decades ago. Morris (1965:244-282) was probably the first worker to use trait incidences (for both upper and lower cuspids) in an intergroup comparison between Papago and Pecos populations. However, the character was not well described or its variation clearly defined by any of these authors.

Scott (1973:27,169-174; 1977a) produced a standard plaque to classify the different degrees of distal accessory ridge expression (see Figure 11a,11b, pp. 113-114) and was the first odontographer to emphasize the importance of the trait in the investigation of intergroup relationships. He found that distal ridge frequencies ranged from 70% - 95% for the upper cuspid in seven Southwestern tribes (ten samples) and were ca. 85% - 90% for the two Euro-American populations. The modal category for degree of expression was between class 2 and class 3; i.e. on the low side of the six-grade scale.

Figure 11a. Distal accessory ridges of canines: basic morphology. (Adapted from Scott, 1977a: Figure 1.)


Upper Canine
medial lingual ridge
mesial marginal ridge
lingual tubercle
distal accessory ridge
distal marginal marginal ridge

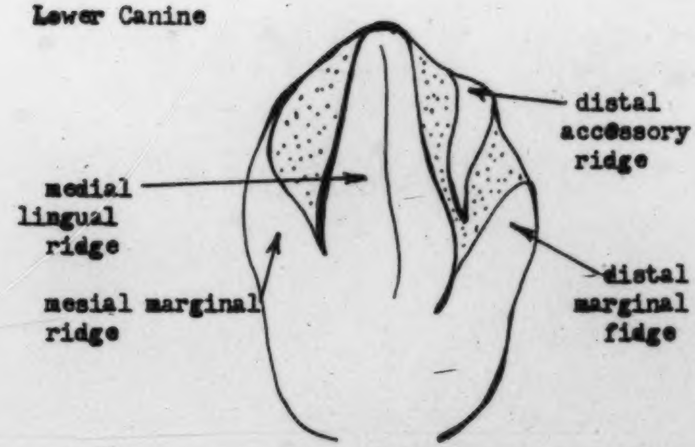
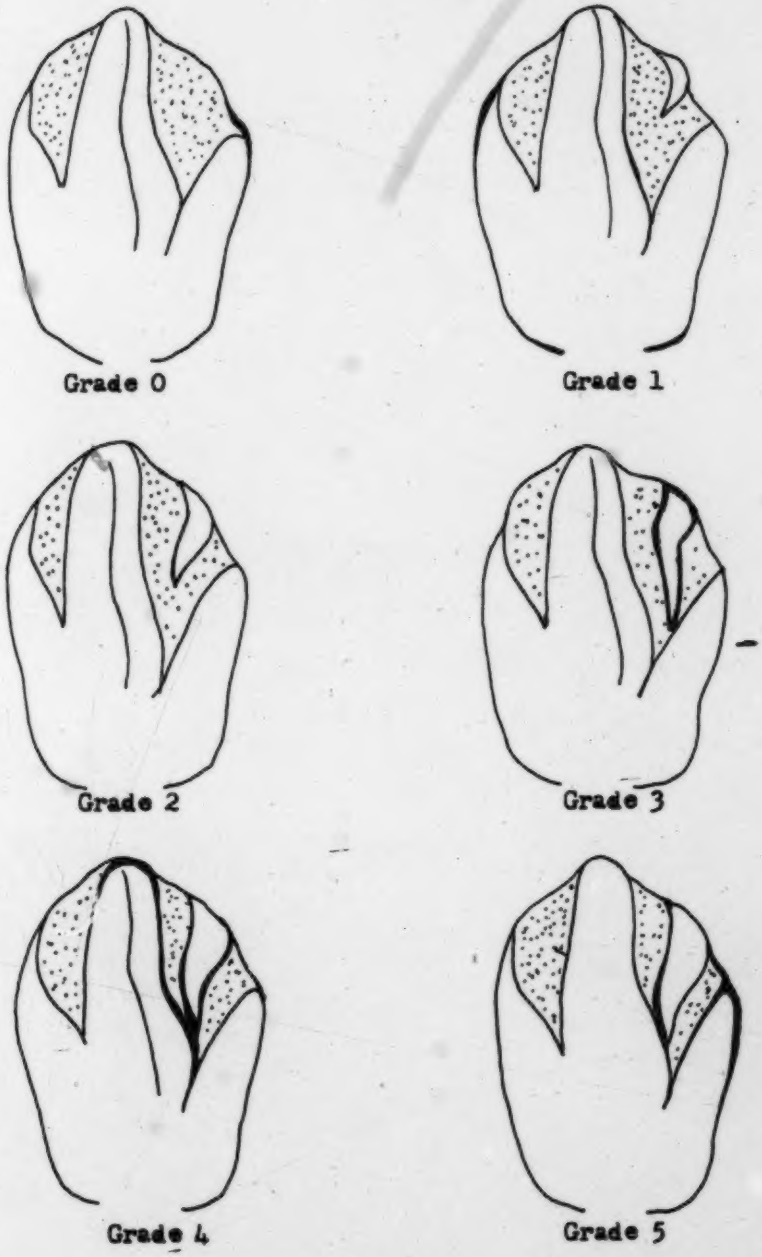

Lower Canine
medial lingual ridge
mesial marginal ridge
distal accessory ridge
distal marginal fidge

Figure 11b. Distal accessory ridge of canines: phenotypic variation. (Adapted from Scott, 1977a: Figure 2.)



Grade 0

Grade 1

Grade 2

Grade 3

Grade 4

Grade 5

The distal accessory ridge was less commonly observed on the lower canine, but showed greater intergroup variation on this tooth (Scott, 1973:169-174; 1977a). Southwestern tribes displayed frequencies of 35% - 75%, with Athapascan populations ranging from 35% - 50% while non-Athapascan populations (with one borderline exception) varied from 55% - 75% in trait incidence. Euro-American and Asio-Indian samples exhibited the distal accessory ridge significantly less often (ca. 20% - 25%) than most Amerindian groups. The modal category for degree of expression was between class 1 and class 2, so that ridge manifestation was weaker than on the upper cuspid.

In the last decade, a number of research papers have confirmed the usefulness of the canine distal accessory ridge for intergroup variation studies. Scott and his coworkers (Scott and Dahlberg, 1982; Scott et al., 1983) have continued their investigations of Southwestern Amerindian dental morphology, using this feature (among others). Kaul and Prakash (1981) have presented figures on cuspid distal ridging for an Asian Jat population. Kieser (1984a; Kieser and Preston, 1981) has given ridge frequencies for the South African Griqua dentitions and the Paraguayan Lengua tribe.

Turner and his coworkers have determined the trait incidence (for C^1) in 15 different "populations" of varying magnitudes, including Mongoloid and non-Mongoloid (e.g. Scandinavian) Holarctic samples, Oriental and Oceanic groups and numerous Amerindian tribes (Turner, 1979; 1985; Turner and Hanihara, 1977; Turner and Swindler, 1978). Turner believes that distal accessory ridging is one of a complex of characters (e.g. shovelling, labial ridging, cingular tuberculation) that strengthen and prolong the utility of the canine crown by adding mass to it, especially with the stronger degrees of expression. These features were possibly selected for during late Pleistocene times in northeastern Asia, under "dentally-demanding, Arctic-like conditions" (Turner, 1985).

Research done on fairly large samples has consistently indicated the presence of marked sexual dimorphism in the frequencies of canine distal accessory ridges. Scott (1973:169) found that the modal class in trait expression for males was usually a grade higher than that for the females, in both upper and lower cuspids. He also determined that most Amerindian samples displayed significant sexual differences in the incidence of distal ridging for the upper cuspid and a few showed these for the lower cuspid (Scott, 1973:56-60; 1977a). Male-female differences in the grade of distal ridging were more pronounced in the maxillary canine while the frequency differences were greater in the mandibular eye-tooth.

Subsequent work has tended to confirm Scott's (1973:56-60; 1977a) initial proposals. Statistically significant sexual differences in canine distal ridge incidence have been observed for a variety of populations, e.g. Asian Jats, Paraquayan Lengua, American Pimas (Kaul and Prakash, 1981; Kieser and Preston, 1981; Scott et al., 1983). Jomon and Grique dentitions did not show marked sexual dimorphism for the trait, but sample sexes were rather small in both cases (Turner, 1979; Kieser, 1984a).

The mode of inheritance of the canine distal accessory ridge is presently uncertain; it is possible that the trait is linked to the X-chromosome and likely that it is polygenic and quasicontinuous in nature (Scott, 1977a; Scott et al., 1983). There is a significant positive association between distal ridging on the upper and lower cuspids. The feature usually occurs bilaterally in both jaws, with a presence-absence asymmetry of ca. 5%.

4.3.2 Methodology for the distal accessory ridge.

As Scott's (1973:27; 1977a) six-grade plaques for maxillary and mandibular canines were not available at the University of Alberta, only a very approximate classification system could be used to categorize the variation in expression found in the distal ridge trait. The ridge manifestations were scored as either weak (grades 1-3) or strong (grades 4-5), according to a basic subdivision of Scott's scale (see Figure 11b, p. 114). Two casts were used as standards, one for each jaw; these represented the maximum degree of weak distal ridging.

Some problems were anticipated in regard to scoring the maxillary canine. These teeth are apparently subject to rapid wear, resulting in a greatly reduced sample size (Kieser and Preston, 1981), and are not as useful in determining intergroup relationships as the mandibular cuspids (Scott, 1973:169; 1977a; Scott and Dahlberg, 1982). However, both teeth (C^1 and C_1) were examined for the distal ridge trait in all Grimsby jaws.

4.3.3 Observations on the distal accessory ridge.

The observations are given in Tables 7a,7b (pp.119-120). The frequency for the distal accessory ridge for the lower canine was determined to be 29.0% (unweighted, n=31%) or 36.3% (weighted for sexual dimorphism); the feature was expressed bilaterally in all determinable cases. However, it was only weakly manifested by the Grimsby population; the strongest expression (approaching a class 3 level) being found in a (probable) male specimen. A statistically significant differnce (x^2=0.011) was found in trait incidence between males (60.0%, n=10) and females (12.5%, n=16).

The distal accessory ridge occurred more commonly on the upper cuspid (85.0%, n=20) than in the lower one. Males displayed a frequency of 100.0% (n=7) for the trait, while the female incidence (70%, n=10) was markedly but not significantly lower. The distal ridge character was usually

TABLE 7a. DISTAL ACCESSORY RIDGE OF CANINES IN THE GRIMSBY SAMPLE: OCCURRENCE BY SIDE.

SEX	MAXILLARY CANINE L SIDE #	 R SIDE #	MANDIBULAR CANINE L SIDE #	 R SIDE #
MALE				
ridge	5	6	5	6
total	6	6	7	10
FEMALE				
ridge	7	3	2	2
total	10	4	12	13
ALL				
ridge	15	11	7	9
total	19	12	23	27

++ Average weighted for sexual dimorphism (male/female frequencies) is 36.3%.

TABLE 7b. DISTAL ACCESSORY RIDGE OF CANINES IN THE GRIMSBY SAMPLE: OCCURRENCE BY INDIVIDUAL.

SEX	MAXILLARY CANINE INDIVIDUAL # (%)	MANDIBULAR CANINE INDIVIDUAL # (%)
MALE		
ridge	7 (100)	6 (60.0)
total	7 (100)	10 (100)
asymmetry	1/7	0/10
FEMALE		
ridge	7 (70.0)	2 (12.5)
total	10 (100)	16 (100)
asymmetry	1/10	0/16
ALL		
ridge	17 (85.0)	9 (29.0)++
total	20 (100)	31 (100)
asymmetry	2/17	0/31

++ Average weighted for sexual dimorphism (male/female frequencies) is 36.3%.

bilaterally manifested; there were two possible cases of unilateral occurrence, but in both specimens, wear was evident on the canine crowns. The strongest expression (approaching a class 3 level) was found in a male specimen.

Wear greatly reduced the usable sample size for both upper and lower canines. In the case of the maxillary teeth, 20 specimens showed marked wear, so that the distal ridge trait could not be scored for one (7) or both (13) sides. In the mandibular cuspids, 30 casts displayed marked wear, so that distal ridging could not be determined for one (9) or both (21) sides. Females exhibited strong bilateral attrition more often (9/13 jaws) in the upper canines while males showed it more commonly (14/21 jaws) in the lower teeth.

4.4 Miscellaneous morphological features of maxillary and mandibular canines.

Lingual marginal ridging in the upper cuspid (see Figure 10, p. 105) is usually not as marked or as common as in the incisors of the same jaw in most populations studied to date, e.g. East Greenland Eskimo, Southwestern Amerindian groups, Jomon, Griqua (Pedersen, 1949:177; Dahlberg, 1951; Turner, 1979; Kieser, 1984a). Canine shovelling incidences have rarely been given in the literature, exceptions being Turner's (1979) paper on the Jomon (100% for all classes on I^1 and I^2 and ca. 70% on C^1) and Kieser's (1984a) study of the Griqua dentitions (100% for all classes on I^1 and I^2 and ca. 90% on C^1). An important problem in grading the feature is caused by the frequent occurrence of a pronounced mediolingual ridge, which may largely obliterate the lingual fossa (Pedersen, 1949:174; Moorrees, 1957:23; Kirveskari, 1974:16).

Marginal ridging in the lower cuspids is generally not as robust as in the upper ones, at least for Euro-American and Eskimo dentitions (Black, 1890:39; 1897:41; Diamond, 1929:91; 1952:120; Pedersen, 1949:174-175). However, in Amerindian teeth, the mandibular canines usually display stronger shovelling than the incisors in the same jaw (Dahlberg, 1951). The trait has been used in interpopulation comparisons of two Southwestern Amerindian tribes (Morris, 1965:244-282) and three Skolt Lapp groups (Kirveskari, 1974:15-21). In the last case, the marginal-ridging incidence (basically, of the "trace" grade) was roughly the same for both cuspids and incisors, ranging from ca. 20% - 45%, depending on the group under consideration.

Sexual dimorphism does not seem to be a factor in lingual marginal ridging frequencies for cuspids. Moorrees (1957:26) remarked that in living Aleut populations, males consistently displayed higher proportions of the stronger degrees of canine shovelling than females, but did not give figures or do statistical tests. In two of Kirveskari's (1974) Lapp groups females had greater shovelling incidences (by ca. 5% - 20%, for C_1), while Kieser's (1984a) Griqua sample showed the same tendency (female frequencies predominating by ca. 20%, for C^1), although males had a higher proportion of strong marginal ridging (ca. 70% to ca. 60%). No significant differences in male-female frequencies were found in either Lapps or Griquas; nor did Turner (1979) find significant sexual dimorphism in his Jomon dentitions (for C^1).

In the absence of "type" plaster plaques, a couple of casts (one upper jaw and one lower jaw) were used as standards for the shovelling feature in the canines. Only marked degrees of ridge and fossa formation were recorded as present; i.e. those cases where the marginal crests were distinctly more protrusive than the mediolingual ridge. Observations were made on both maxillary and mandibular cuspids.

Marked shovelling was rare (12.0%, 3/25) in the upper canine, because of the common occurrence of a robust mediolingual ridge. The lower cuspids generally displayed very weak ridge and fossa formations, which usually fell between the trace and absent grades. The distal marginal ridge tended to be more pronounced than the mesial one. Shovelling was bilaterally manifested and significant sexual differences in trait incidence was not found.

CHAPTER 5.

MAXILLARY AND MANDIBULAR PREMOLARS.

5.1 Introduction.

In this section, attention will be focused on four anatomical characters: cusp number, occlusal surface pattern, transverse ridge form and occlusal accessory ridge number. The first two features are associated to some degree and will be considered together for the two mandibular premolars (P_3 and P_4). Transverse ridge form and occlusal ridge number are also related, as both contribute to the total occlusal ridge number; these two traits will be discussed in the same subsection for both lower bicuspids.

Intergroup comparisons using premolar traits are a rather recent occurrence in dental anthropology. Kraus and Furr (1953) pointed out the potential value of several characters on the first lower bicuspid, and Ludwig (1957) made similar remarks with regard to features on the second mandibular premolar. Morris (1965:51-53, 244-282) used many of these suggested traits in his examination of the relationships of living and skeletal American Southwest tribal populations. Scott (1973:27-28,32-33,174-177,189-196) employed pre-molar cusp number and occlusal ridging in his comparison of several Southwest native and white populations. Scott and Dahlberg (1982) and Turner (1983; 1985; 1987) have used lingual cusp-number frequencies in their studies of Amerindian, Asiatic and European groups. Mayhall et al. (on P_4) (1982) have examined both cusp number and surface pattern in modern Euro-American dentitions.

Another feature believed to have some discriminatory value at the demic and racial level is the "occlusal tubercle" or "axial core adontome" which is considered by some workers to be a diagnostic Mongoloid trait (see Tratman 1949; Lau, 1955; Merrill, 1964; Mayhall, 1979b). Turner (1985; 1987) has recently used the frequency of this character on both maxillary and mandibular premolars in his comparative analysis of Amerindian and Oriental populations. In this thesis, both lower bicuspids were examined for the presence of the occlusal tubercle, and teh relevant data is given in a "Miscellaneous morphological features" subsection at the end of the chapter.

Maxillary premolars tend to be regular in their occlusal groove pattern and general crown anatomy (Kraus et al., 1969:57-61). In most populations examined so far, they have been consistently bicuspid, e.g. East Greenland Eskimo, Jomon, Euro-American, Griqua (Pedersen, 1949:129; Turner, 1979; Mayhall, et al., 1982; Kieser, 1984a). Some observations on maxillary premolar morphology were made, and upper bicuspid crowns were examined for the presence of premolar occlusal tubercles. This data is presented in the "Miscellaneous morphological features" subsection.

5.2 Cusp number and occlusal surface patterns of the mandibular premolars.

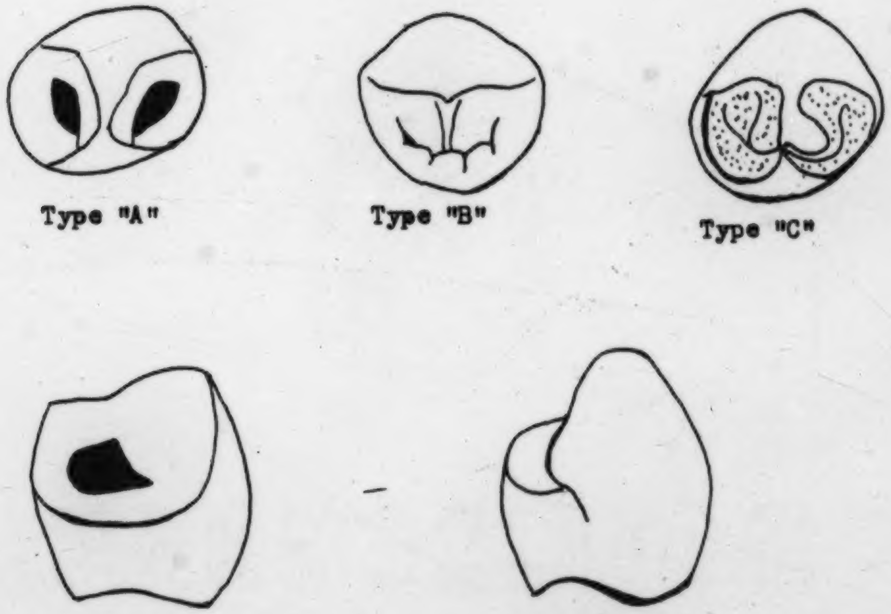
5.2.1 Various aspects of cusp number and occlusal surface patterns.

The first premolars of hominid forms are generally bicuspid, although this has not always been true in the past (Leonard and Hegman, 1987). Kraus et al. (1969:71) have described three different types of lower first premolar crown, to which two others have been added here (see Figure 12a, p. 126). This system was based loosely on buccal cusp size and transverse ridge form.

A major problem with cusp counting for the anterior bicuspid is that supernumerary lingual elements are usually small nodules rather than well-defined cusps (Scott, 1973:32-33, Scott and Dahlberg, 1982). These tiny tubercles are often incidental to the main pattern of multiple lingual cusp manifestation and may reflect random secondary events during tooth formation (Scott, 1973:32-33; Scott and Dahlberg, 1982; Scott et al., 1983). This situation also exists for the posterior premolar, but to a minor degree, because distinct lingual cusps in this tooth are larger and much more commonly observed (Pedersen, 1949:129,162-165; Moorrees, 1957:31; Scott and Dahlberg, 1982).

The second mandibular premolar is usually bicuspid or tricuspid, rarely quadricuspid, with the number of lingual elements varying from one to three (see Figure 12b, p. 127). The buccal cusp is markedly larger than the lingual ones; of

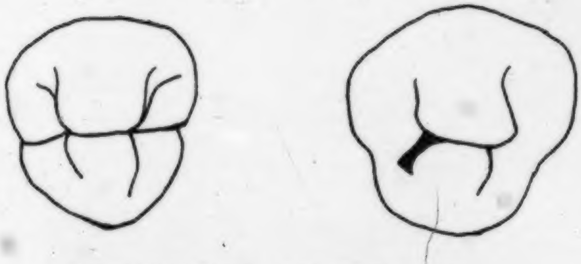
Figure 12a. Occlusal form of mandibular premolars: first premolar types. (Adapted from Kraus et al., 1969:71.)



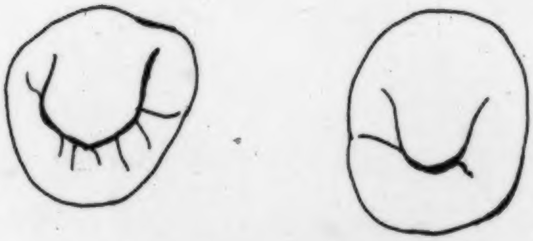
Type "A" Type "B" Type "C"

Type "A" Type "B"

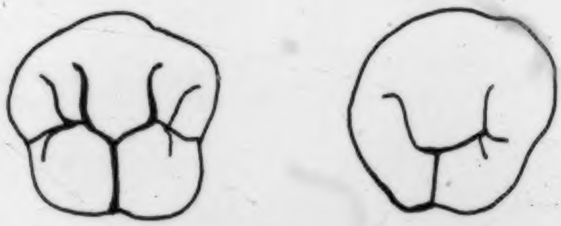
Figure 12b. Occlusal form of mandibular premolars: second premolar types. (Adapted from Zeisz and Nuckolls, 1949:172, Figures 155-157.)



Type "H" form and variation.



Type "U" form and variation.



Type "Y" form and variation.

the latter, the mesiolingual element is usually larger than the distolingual when both are manifested (Kraus et al., 1969:69-70; Mayhall et al., 1982; Scott and Dahlberg, 1982). The distolingual cusp or cusps range from a state of absence to a tubercle which may (very rarely) be larger than the mesiolingual element (Scott, 1973:32-33; Scott et al., 1983).

Research involving the lingual multicusp trait has so far demonstrated that the occurrence (percentage) of this character does not separate the major geographic races (Turner, 1967b:53; 1985). Various Caucasoid populations have been found to vary from ca. 15% to ca. 65% in tricuspid second premolar frequencies (Pedersen, 1949:162; Ludwig, 1957; Scott and Dahlberg, 1982; Mayhall et al., 1982; Woelfel, 1984:119; Turner, 1985), while the incidence for one Negroid group was reported to be ca. 40% (Ludwig, 1957). The proportions of multicusped premolars in peoples of Mongoloid affinities range from a low of ca. 15% in the Hopi tribe to a high of ca. 85% in northeast and southeast Asians (Scott and Dahlberg, 1982; Turner, 1985).

However, Mongoloid populations do seem to show some evidence of microgeographic patterning of tricuspid premolar frequencies. American Arctic groups (Eskimo, Aleut, Athapascan) vary from ca. 30% to ca. 50% (Pedersen, 1949:129; Turner, 1967b:57; 1983, 1985) with the single exception of Moorrees' (1957:30) possibly hybrid Aleut sample (ca. 20%). American Southwest tribes have an incidence range of ca. 15% to ca. 30% for multicusped premolars, e.g. Hopi, Apache, Pima, Navajo, Papago, Yuma, Zuni, Mohave (Scott and Dahlberg, 1982; Scott et al., 1983). Asian Arctic populations display even higher proportions of this feature (ca. 45% - 85%) than American Arctic groups, e.g. northeastern Siberians, Ket, Amur Basin dwellers, northeastern Asians. Multicusped premolars are most commonly observed (ca. 65% - 85%) in southeastern Asian peoples, e.g. Balinese, Jomon, other "Sunda" groups (Jacob, 1967; Turner, 1979, 1985, 1987).

Groove-pattern frequencies have not been as widely investigated or reported as cusp-number incidence. Black (1890:54-55; 1897:56-57) described the three basic occlusal-surface types, i.e. the "H", "U" and "Y" variations, for the second premolar (see Figure 12b, p. 127), but these were not actually labelled as such until some time later (Zeisz and Nuckolls, 1949:161,175). The first two configurations are associated with bicuspid teeth, while the last is invariably found on tricuspid antimeres. Kraus et al. (1969:69,73-74) have remarked that the "Y" pattern is usually observed in the second premolars of American (white?) populations. However, Mayhall et al. (1982) found that in their Euro-American sample, the "H" configuration was the most common one (ca. 50%), while the "Y" and "U" types (ca. 35% and ca. 15%, respectively) were less often encountered.

Cusp and groove pattern frequencies apparently do not display sexual dimorphism. Statistically significant differences for male-female incidences of multicusped premolars have not been found in populations examined to date, e.g. Aleut, Eskimo, Athapascan, Jomon, Euro-American, Pima (Moorrees, 1957:30-31; Turner, 1967b:51-52; 1979; Mayhall et al., 1982; Scott et al., 1983). Mayhall et al. (1982) determined that occlusal surface configurations were not sexually dimorphic in their Euro-American sample.

5.2.2 Methodology for occlusal surface patterns.

In scoring cusp number, any element with a completely independent apex was recorded as a cusp, in accordance with the definition used by P.J. Wright (1974:38) and K.E. Wright (1977:25). However, a distinct groove between the lingual elements was also required in order for a third cusp to be clearly recognized; while this was not specifically mentioned by P.J. Wright or K.E. Wright, it is clearly evident in the illustrations given by their standard source (Kraus et al., 1969:71-74). Occlusal surface patterns were identified as "H2", "U2" or "Y3", or variations of these (see Figure 12b, p. 127) for the posterior bicuspid, except for unusual or irregular groove-configurations, which were placed in a fourth category.

In regard to the first premolar, the occlusal surface types illustrated in Figure 12a (p. 126) were used for classification purposes. Also, the height advantage of the buccal cusp over the lingual element was used to independently place each tooth in a metric category. These categories were: 0-2 mm, 2-3 mm, and 3-4 mm.

5.2.3 Observations on occlusal surface patterns.

The observations are given in Tables 8a,8b, pp. 134-135. The dominant occlusal surface pattern in the anterior premolars was the "D" type (44.9%), with the "A" and "C" types also being of some significance (18.4% and 16.3%, respectively). The "D" type premolars manifested a tremendous range in occlusal outline, including subcercular, oval, subtrapezoid, lenticular, piriform, and lopsided forms, as did the "E" type, but to a lesser degree. the "A" and "D" type bicuspids fell into the lowest metric class of buccal cusp superiority (0-2 mm) with very few exceptions. Specimens belonging to the "B" and "C" types generally fell into highest-metric class (3-4 mm) while those belonging to the small "E" category fell into all three metric classes.

Usually, two distinct cusps were manifested in the case of the anterior premolars. However, Fe27#345 showed only a slight lingual bulge where the cusp would generally have been found, while Fe27#34 lacked the lingual element entirely. Fel#27 displayed only two small cuspules on the marginal palatal margin of a large conoid buccal element.

TABLE 8a. OCCLUSAL SURFACE FORM OF MANDIBULAR PREMOLARS IN THE GRIMSBY SAMPLE: FIRST PREMOLAR TYPES.

SEX	L SIDE #	R SIDE #	INDIVIDUAL # (%)
MALE			
A	3	3	4 (17.4)
B	0	0	0 (0.0)
C	4	4	4 (17.4)
D	12	10	12 (52.2)
E	1	1	1 (4.3)
A/D	2	2	2* (8.7)
total	22	20	23 (100)
FEMALE			
A	5	5	5 (23.8)
B	2	2	2 (9.5)
C	2	3	3 (14.3)
D	8	6	9 (42.9)
E	1	1	1 (4.8)
A/D	1	1	1 (4.8)
TOTAL	19	18	21 (100)
ALL			
A	8	8	9 (18.4)
B	2	3	3 (6.1)
C	7	8	8 (16.3)
D	21	17	22 (44.9)
E	4	4	4 (8.2)
A/D	3	3	3 (6.1)
total	45	43	49 (100)

*One specimen actually shows "D" on LP and "A" on RP_3.

TABLE 8b. OCCLUSAL SURFACE FORM OF MANDIBULAR PREMOLARS IN THE GRIMSBY SAMPLE: SECOND PREMOLAR TYPES.

SEX	L SIDE ￼#	R SIDE ￼#	INDIVIDUAL ￼# (%)
MALE			
H2	6	6	7 (35.0)
U2	5	2	5 (25.0)
Y3	1	2	2 (10.0)
misc.-2	3	4	4 (20.0)
H2/U2	1	1	1 (5.0)
U2/Y3	1	1	1 (5.0)
total	17	16	20 (100)
FEMALE			
H2	7	6	8 (33.3)
U2	3	4	5 (20.8)
Y3	3	2	3 (12.5)
misc.-2	6	7	7 (29.2)
H2/U2	0	0	0 (0.0)
U2/Y3	1	1	1 (4.2)*
total	20	20	24 (100)
ALL			
H2	14	13	16 (33.3)
U2	8	6	10 (20.8)
Y3	5	5	6 (12.5)
misc.-2	10	12	12 (25.0)
H2/U2	2	2	2 (4.2)
U2/Y3	2	2	2 (4.2)
total	41	40	48 (100)

* Specimen actually shows "Y3" on LP_4 and "U2" on RP_4.

No marked sexual dimorphism was observed for either cusp number or the occlusal surface variations.

The bicuspid types were dominant in the Grimsby sample, with the "2" configuration and its variations forming the largest groups (33.3%, n=48), followed by the irregular (2-cusped) and "U2" categories (25.0% and 20.8%, respectively). The tricuspid "Y3" frequency was relatively low (12.5%). There were also four individuals (8.3%) who displayed lateral asymmetry (viz. H2/U2 or U2/Y3 combinations of patterns). No marked sexual dimorphism was observed for either cusp number of the occlusal surface variations.

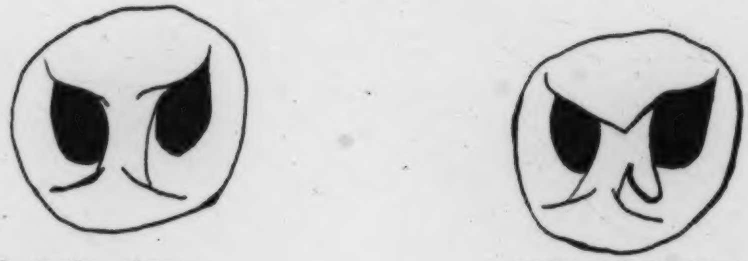
5.3 Occlusal transverse ridges on the mandibular premolars.

5.3.1 Various aspects of occlusal transverse ridges.

The occlusal surface of the mandibular premolars is usually crossed by a distinct transverse (buccolingual) ridge. This ridge lies across the central portion of the surface and may be simple or bifurcated in form (see Figure 13, p. 136). There may also be mesial or distal accessory ridges running more or less parallel to the primary transverse crest (Kraus and Furr, 1953; Kraus, 1957; Ludwig, 1957; Kraus et al., 1969:71-74,293-294).

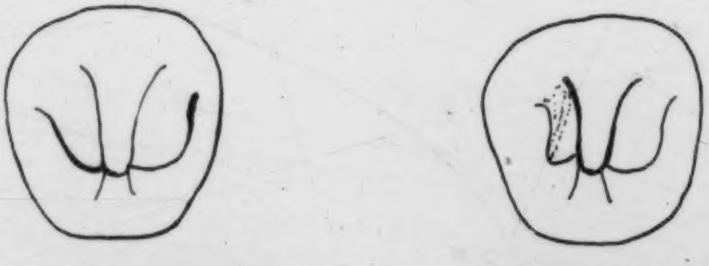
Occlusal ridge traits have not been widely used in intergroup comparisons. Kraus (1957) found that Euro-Americans generally had only one (30%) or two (46%) ridges on their first lower bicuspids, while Chinese populations as

Figure 13. Occlusal transverse ridges on mandibular premolars.



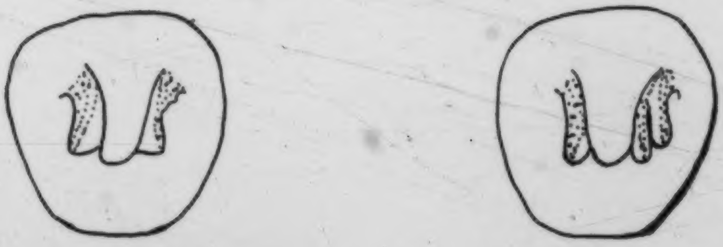
simple ridge

bifurcated ridge



0 accessory ridges

1 accessory ridge (mesial)



2 accessory ridges (mesial and distal)

3 accessory ridges

often as not had three (50%), and teh Arizona Papago had a relatively high incidence (32%) of four-ridged teeth. Morris (1965:244-282) used occlusal ridge number on both premolars in his comparison of living Papago and skeletal Pecos samples.

5.3.2 Methodology for occlusal transverse ridges.

Morris (1965:53) and P.J. Wright (1974:38-39) gave figures for primary transverse-ridge form (simple or bifurcated) and also for total occlusal-ridge number. For total ridge counts, the primary crests were lumped together with accessory ridges; the former were considered as two ridges when bifurcated (following Kraus and Furr, 1953, and Kraus et al., 1969:289). Kraus et al. (1969:289) listed the primary ridge form as a trait separate from accessory ridge number, although they included both primary and accessory crests in their occlusal ridge counts. The procedure followed here was similar to that accepted by K.E. Wright (1977:26), who presented separate statistics for the form of the primary ridge and for accessory ridge number.

5.3.3 Observations on occlusal transverse ridges.

The observations are given in Table 9a,9b, pp. 138-139. The proportions of simple and bifurcated ridges were very similar for both mandibular premolars, with the simple type predominating by a ratio of about three to one (in P_3,

TABLE 9a. OCCLUSAL TRANSVERSE RIDGES ON MANDIBULAR PREMOLARS IN THE GRIMSBY SAMPLE: OCCURRENCE BY SIDE.

	FIRST PREMOLAR		SECOND PREMOLAR	
SEX	L SIDE #	R SIDE #	L SIDE #	R SIDE #
MALE				
prim. rdg.				
simple	18	16	14	14
bifurcated	3	2	2	1
0acc.rdg.	6	3	4	0
1acc.rdg.	7	8	6	9
2acc.rdg.	8	7	5	6
3acc.rdg.	0	0	1	0
total	21	18	16	15
asymmetry				
FEMALE				
prim. rdg.				
simple	13	14	15	15
bifurcated	6	4	4	5
0acc.rdg.	7	7	10	8
1acc.rdg.	9	7	4	4
2acc.rdg.	2	4	5	8
3acc.rdg.	1	0	0	0
total	19	18	19	20
asymmetry				
ALL				
prim. rdg.				
simple	35	35	31	32
bifurcated	9	6	8	7
0acc.rdg.	16	12	15	10
1acc.rdg.	16	16	12	14
2acc.rdg.	11	13	11	15
3acc.rdg.	1	0	1	0
total	44	41	39	39

[ ] Presence-absence trait asymmetry.

TABLE 9b. OCCLUSAL TRANSVERSE RIDGES ON MANDIBULAR PREMOLARS IN THE GRIMSBY SAMPLE: OCCURRENCE BY INDIVIDUAL.

SEX	INDIVIDUAL # (%)	INDIVIDUAL ~~# (~~%)
MALE		
prim. rdg.		
simple	19 (86.4)	16 (84.2)
bifurcated	3 (13.6)	3 (15.8)
0acc.rdg.	3 (13.6)	4 (21.1)
1acc.rdg.	9 (40.9)	8 (42.1)
2acc.rdg.	10 (45.5)	6 (31.6)
3acc.rdg.	0 (0.0)	1 (5.3)
total	22 (100)	19 (100)
asymmetry		
FEMALE		
prim. rdg.		
simple	14 (66.7)	17 (73.9)
bifurcated	7 (33.3)	6 (26.1)
0acc.rdg.	7 (33.3)	9 (39.1)
1acc.rdg.	9 (42.9)	5 (21.7)
2acc.rdg.	4 (19.0)	9 (39.1)
3acc.rdg.	1 (4.8)	0 (0.0)
total	21 (100)	23 (100)
asymmetry	3/21	4/23
ALL		
prim. rdg.		
simple	37 (78.7)	35 (76.1)
bifurcated	10 (21.3)	11 (23.9)
0acc.rdg.	12 (25.5)	14 (30.4)
1acc.rdg.	18 (38.3)	15 (32.6)
2acc.rdg.	16 (34.0)	16 (34.8)
3acc.rdg.	1 (2.1)	1 (2.2)
total	47 (100)	46 (100)
asymmetry	10/47 [6]	7/46 [3]

[ ] Presence-absence trait asymmetry.

78.7% to 21.3%, n=47; in P_4, 76.1% to 23.9%, n=46). In both teeth, one or two accessory ridges were usually found (38.3% and 34.0% for P_3, n=47; 32.6% and 34.8% for P_4, n=46). Three accessory ridges were only rarely observed (ca. 2%) on the lower bicuspids. Accessory occlusal transverse ridges were absent in a significant fraction of the Grimsby premolar sample (25.5% for the P_3; 30.4% for the P_4). Marked discrepancies in male-female frequencies were not found in either tooth.

Some difficulty was encountered in scoring occlusal ridge number. Accessory ridges varied markedly in length and prominence, and also in orientation on the occlusal surface. In many cases, accessory ridges lay parallel to the primary transverse crest; however, in several instances, they ran at an acute angle to the latter feature. Accessory ridges were counted as "transverse" elements when their major direction was buccolingual rather than mesiodistal.

In regard to primary ridge asymmetry, females were more likely to display simple/bifurcated combinations (scored as "bifurcate") than males, on both the first (2/7 bifurcated specimens) and second (3/6 bifurcated specimens) premolars. The males did not show lateral trait asymmetry for either premolar. Overall trait asymmetry was 20.0% (2/10) for bifurcated first premolars and 36.4% (4/11) for bifurcated second premolars.

For the accessory ridge trait, males showed nearly twice the asymmetry frequency of females (27.3% or 6/22 to 14.3% or 3/21) for the first bicuspid. However, males showed only about half the female incidence for the second tooth (10.5% or 2/19 to 17.4% or 4/23). The overall trait asymmetry was somewhat higher in the first premolar (21.3%, or 10/47) than in the second element (15.2%, or 7/46). Antimeric discordance was only a single grade for both premolars.

5.4 Miscellaneous morphological features of maxillary and mandibular premolars.

The maxillary premolars were strongly bicuspid and virtually identical in shape. The single exception was a "barrel" right second premolar in one female specimen (Fe62#61). The unusual shape of this tooth was apparently due to crowding during crown formation; the opposing antimere was regular in its morphology.

Premolar occlusal tubercles are protuberances occurring more or less in the central portion of the occlusal surface. These features consist of enamel, dentine and generally, a pulp chamber (Lau, 1955; Ochlers, 1956; Mayhall, 1972). According to Mayhall (1979b), tuberculated bicuspids vary in their occurrence from 0% (Sadlermiut Eskimos) to 38% (Koyukon Amerindians) among Mongoloid populations. The trait is rare or absent in other racial groups (Lau, 1955; Mayhall et al., 1982). The Grimsby specimens were examined for occlusal tubercles, but none were found on either the maxillary premolars (P^3 n=56; P^4 n=56) or the mandibular ones (P_3 n=51; P_4 n=51).

CHAPTER 6.

MAXILLARY MOLARS.

6.1 Introduction.

This section will focus mainly on cusp number and accessory lateral tubercles, and will include a discussion of the anatomy, phylogeny, racial variation and genetic aspects of these features. Cusp number is closely associated with several other characters, namely hypocone reduction, distal tubercle expression, and supernumerary occlusal elements. These traits and modifications will therefore be considered together.

The best known accessory element is the Carabelli tubercle, the strongest expression of a rather variable trait. This is probably the most intensively investigated anatomical character in the dental literature. In contrast, paramolar and other extra cusps have seldom been studied.

Research papers in dental anthropology have usually dealt only with cusp number (or hypocone reduction) and the Carabelli trait when considering the upper molars (e.g. Dahlberg, 1951; 1963a; Moorrees, 1957:32-41; Turner, 1969a; Sofaer et al., 1972b; Kirveskari, 1974:29-38; Baume and Crawford, 1980), although occasionally miscellaneous minor features have also been examined (Morris, 1965:244-282). In the last two decades, several authors have included distal tubercle expression and frequency in their studies (Turner, 1967b:96-102; 1979; 1983; 1985; 1987; Scott, 1973:186-189; Scott and Dahlberg, 1982; Scott et al., 1983). Recent investigations into the manifestation and racial occurrence of the upper paramolar tubercles have largely been carried out by two individual workers (Kustaloglu, 1962; and Turner, 1967b:96-102; 1983; 1985; 1987).

6.2 Occlusal surface features of maxillary molars: hypocone expression and distal tubercle character.

6.2.1 Anatomical description and phylogeny of hypocone expression.

The hypocone is the most recent (fourth) cusp to be added in the evolution of the upper primate dentition, and it is generally the last to appear embryonically (Kraus and Jordan, 1965:121-122; Kraus et al., 1969:83-85,297-298; Kirveskari, 1974:29-30). Dental anatomists have noted (in studies of Caucasoid populations) that hypocone reduction tends to increase from the first molar to the last, in the same individual (Black, 1890:65,68; 1897:67,70; 1894:67-68, 77; Hellman, 1928; Wheeler, 1940:217; 1974:246;Dahlberg, 1963a; Kraus et al., 1969:74-75). The anterior element almost invariably has four well-developed cusps (i.e. is "fully" quadricuspid); the middle one most commonly displays some significant degree of hypocone reduction, while the posterior tooth is usually tricuspid, or tricuspid with a small distolingual cuspule (see Figure 14a,b,c, pp. 145-147).

Figure 14a. Occlusal surface features of maxillary molars: basic morphology. (Adapted from Dahlberg, 1951:168.)

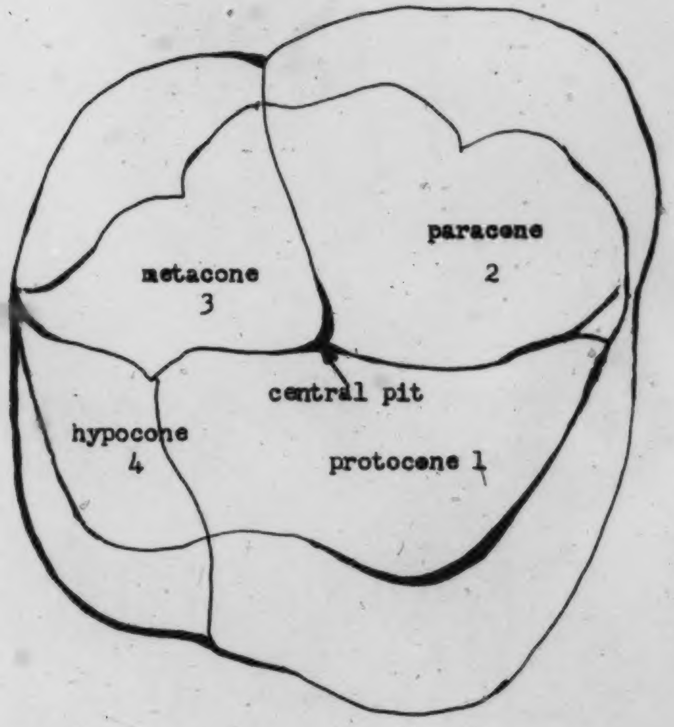

paracone
2
metacone
3
central pit
hypocone
4
protocone 1

Figure 14b. Occlusal surface features of maxillary molars: hypocone expression. (Adapted from Dahlberg, 1951: 168, Figure 6).

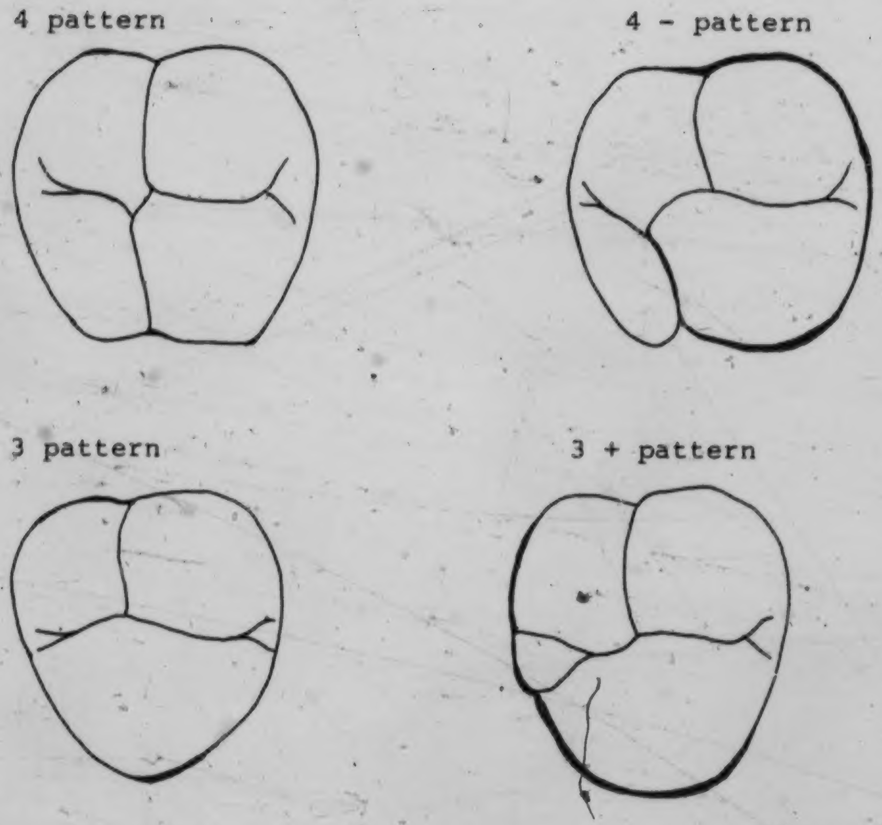
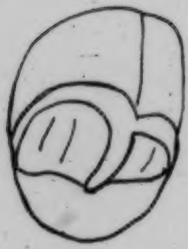
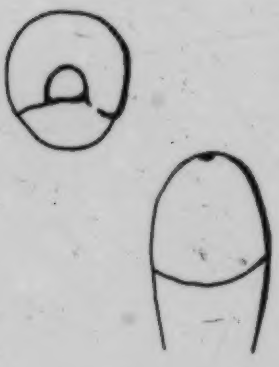

4 pattern
4 - pattern
3 pattern
3 + pattern

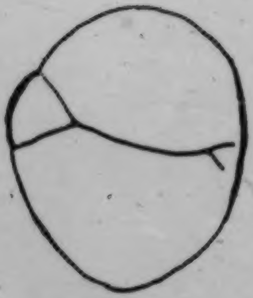
Figure 14c. Occlusal surface features of maxillary molars: reduced teeth - Grimsby specimens.



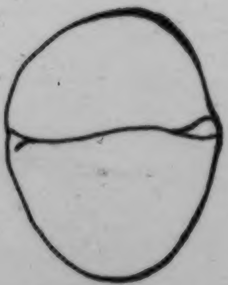
Peg-like bicuspid.
(Based on Fe9#9 - LM^3.)



Uni-cusped peg.
Based on Fe1#27 - RM^3.



2+ form.



Bicuspid.

This pattern of increasing hypocone diminution from front to back has a long history within the Hominidae and is also found in recent pongids (Keith, 1913; Schuman and Brace, 1954). It is displayed by South African australopithecine dentitions (of both gracile and robust types), although tricuspid molars are not observed (Robinson, 1956:87, 96) and fourth cusp reduction is usually relative (to the total occlusal surface area) rather than absolute (Sperber, 1975:62,76,89). The hypocone is also reduced in Oriental pithecanthropines, especially in the third molars (Weidenreich, 1937a:74) and neanderthals often show marked fourth cusp diminishment in the two posterior molars (Bay, 1958; Dahlberg, 1962). The modern pattern of hypocone reduction is also clearly expressed in Neolithic and Megalithic French, Belgian and Swiss populations, although a significant lessening of cusp number has occurred in western Europeans during the last several millenia (Brabant, 1971).

6.2.2 Racial and geographic variation in hypocone expression.

The pattern of hypocone diminution seen in modern Caucasoids has also been observed for other racial groups. Studies of fourth-cusp reduction in all three molars have been made for Amerindian populations, e.g. Pecos Pueblo, prehistoric Texan Pima, northern Athapascan (Nelson, 1938; Goldstein, 1948; Dahlberg, 1951; Turner, 1967b:61,65) and Eskimoid groups, e.g. samples from Greenland, Labrador, Sadlermiut Isle, Arctic Coast, Alaska, Kodiak Isle, Aleutian Islands (Hellman, 1928; Pedersen, 1949:129-130; Dahlberg, 1951; 1963a; Moorrees, 1957:32-34; Turner, 1967b:61-65). The same type of hypocone diminishment from the anterior molar to posterior one has been found in some Oriental peoples, e.g. Balinese, Joman (Jacob, 1967; Turner, 1979) and Melanesian Islanders (Dahlberg, 1945b).

The lack of a single, widely accepted multigrade scale with standardized categories makes the older studies of hypocone diminution of limited value for comparative purposes. Many workers simply classified upper molars as tricuspid or quadricuspid, e.g. Goldstein (1948); Pedersen (1949:129-130); Moorrees (1957:32-34). Some attempted to estimate the degree of distolingual element reduction, and added an intermediate (3+ or 4-) category (e.g. Hellman, 1928; Nelson, 1937; Dahlberg, 1945b). Both Moorrees (1957:35) and Kirveskari (1974:32) have noted the problems involved in comparing investigations which used different classificatory systems.

Recent papers dealing with hypocone reduction have generally used Dahlberg's (1951) scale and the Zoller Laboratory (1956) plaques P#9 and P#11, and are comparable with due regard for interobserver error (Kirveskari, 1974:30-31). Some modern authors, however, have chosen to lump two or more categories together (e.g. Turner, 1983a; 1985; 1987; Scott and Dahlberg, 1982). Sofaer et al.

(1972b) simply scored the fourth cusp as present or absent; Brabant (1971) did not specify what standards he used.

Hypocone reduction in the first upper molar does not serve to distinguish the different geographic races. Amerindian, Eskimoid and Oriental populations show very high proportions of ca. 60% - 100% for the full-quadricuspid grade, while Caucasoid samples show lower but overlapping frequencies of ca. 55% - 80% (Dahlberg, 1951; 1963a; Jacob, 1967; Turner, 1967b:65; 1979; Snyder et al., 1969; Kirveskari, 1974:30; Scott and Dahlberg, 1982; Scott et al., 1983). Tricuspid and near-tricuspid (3+) categories total under 5% for all groups except the Kaguyak Eskimo (Dahlberg, 1963a).

A similar overlap of hypocone-grade proportions for the major racial divisions is evident in the upper second molar. The fourth cusp is usually significantly or markedly reduced, with 4- grade frequencies generally predominating (ca. 30% - 70%) in Amerindian and Oriental populations and 3+ grade frequencies (ca. 20% - 70%) in Eskimoid groups (Dahlberg, 1951; 1963a; Jacob, 1967; Turner, 1967b:65; 1969a; 1979; Snyder et al., 1969; Scott et al., 1983). Caucasoid samples show no consistent tendency, with 4- grade proportions ranging from ca. 10% - 45% and 3+ grade proportions from ca. 15% - 55% (Dahlberg, 1963a; Kirveskari, 1974:30; Mayhall et al., 1982). Among Amerindians, the incidence of tricuspid molars (10% - 45%) is invariably higher than that for full-quadricuspid teeth (ca. 0% - 20%), while Euro-American samples show the opposite tendency, with full-quadricuspid proportions (ca. 25% - 50%) being greater than tricuspid frequencies (ca. 15% - 35%).

The hypocone reduction trait of the upper molars (particularly M^2) seems to be of most value for microgeographic racial comparisons. Significant differences in the pattern of hypocone reduction (using all four grades of Dahlberg's scale) have been found between two Alaskan Eskimo populations (Bang and Hasund, 1973) and two Finnish Lapp samples (Kirveskari, 1974:31-32) for the second molar but not the other two. A number of studies have used only the second molar for comparing or describing closely related American aboriginal groups, e.g. living and extinct Koniag, living and extinct Hopi (Turner, 1969a); Papago, Pima and Zuni (Sofaer et al., 1972b). Marked differences have been observed in fourth-cusp grade-frequencies between living eastern and western Aleuts (Moorrees, 1957:32-34) and skeletal eastern and western Aleuts, and several Eskimo samples (Turner, 1967b:61-65).

The third upper molar is extremely variable and idiosyncratic in its morphology, and probably of limited value in population comparisons at any level. Among Caucasoid groups, it may be absent, present but unerupted, or vary in form from a small, single cusped "peg" to a massive, eight-cusped element (Black, 1890:75; 1897:77; Kraus et al., 1969:94). Kraus et al. (1969:94) have remarked that in white samples the third molar displays much less regularity in structure and development than in "primitive peoples of the world." However, Pedersen (1949:82-84, 126-129) found that this tooth also showed great variability in the East Greenland Eskimo, ranging from a peg-form to a large, five or six-cusped specimen. Data from Dahlberg (1951) and Turner (1983, 1985) indicate that the posterior upper molar can show marked variation in shape and size in some Amerindian and Oriental groups.

The most common "aberrant" form of Mongoloid third molar is probably the unicuspid "peg" element (see Figure 14c, p. 147). Pedersen (1949:84, 128) remarked that "real vestigial specimens" occurred more often in modern Eskimos than whites. According to Turner's (1983) study, Aleut-Eskimo populations had an average peg incidence of 8.2%, while Athapascan and assorted non-Athapascan groups had somewhat lower proportions (2.4% and 3.8%, respectively). Dahlberg (1951) recorded frequencies of 8.3% for a northwest Eskimo cranial series and 4.0% for a Pima sample. Turner (1983; 1985; 1987) believes that peg incidences (and associated third molar agenesis proportions) are of value in inter-population analyses and comparisons.

Recent studies indicate that the third molars of Mongoloids and Caucasoids have generally undergone marked reduction, with the 3+ and 3 grade forming the dominant categories. The cuspule-hypocone frequencies of different racial groups overlap considerably; the incidence-range for Aleut-Eskimo is ca. 0% - 65%; for Pima and Athapascan Amerindians, ca. 10% - 50% (Dahlberg, 1951; Turner, 1967b:65); for some Oriental samples, e.g. Balinese, Jomon, ca. 30% - 75% (Jacob, 1967; Turner, 1979) and for a Euro-American population, ca. 45% (Dahlberg, 1963a). Tricuspid proportions showed a similar overlap among the different groups examined: 0% - 100% for Aleut-Eskimo; ca. 35% - 70% for some Amerindians; ca. 20% - 50% for two Oriental samples and 0% for one Euro-American populations.

Full-quadricuspid teeth (M^3) are found only in very low frequencies in Mongoloids (ca. 0% - 10%) and Caucasoids (ca. 15%). However, this grade-type predominates in Bushmen (Drennan, 1929) and Australoids (Abrahams, 1950; Bailit et al., 1968). Aside from these two groups, it seems to be uncommon in modern man (Kirveskari, 1974:33).

6.2.3 Lateral asymmetry and genetic aspects of hypocone expression.

Lateral asymmetry in hypocone grade-expression seems to vary widely, with the population under consideration. Turner (1967b:60-61) found lateral grade-asymmetry for the two posterior molars (and by implication, the more stable M^1) to be less than 5% for his American Arctic samples. However, Baume and Crawford (1980), using the same standards, viz. Dahlberg's (1956) plaque and scale, observed a much higher incidence of lateral asymmetry for four Mexican (predominantly Amerindian) groups: ca. 6% - 11% for the first molar and ca. 10% - 17% for the second one. Their hybrid Carib and Creole populations also showed higher frequencies of grade-asymmetry (ca. 10% - 15%) for the two anterior molars. The degree of discordance was usually low, i.e. one or two ranks.

Most populations examined to date manifest little or no sexual dimorphism in hypocone grade frequencies. Females generally show a greater reduction in hypocone size and cusp number for the anterior molars (M^1 and M^2), e.g. among living Aleuts, Sadlermiut and west Greenland Eskimos, Mestizos and Tarahumara, Skolt Lapps, Euro-Americans and Pimas (Moorrees, 1957:33,35; Turner, 1967b:65; Snyder et al., 1969; Kirveskari, 1974:31-32; Mayhall et al., 1982; Scott et al., 1983). However, in a few groups, males display greater diminution of the fourth cusp, especially for the first molar; e.g. among Arctic Coast Eskimos, skeletal Aleuts, two small Athapascan samples (Turner, 1967b:65) and several American Southwest tribes (Scott and Dahlberg, 1982).

Significant sex differences in grade-frequency pattern have been found in the first molar of some (pooled) American Arctic populations (Turner, 1967b:58,60), in the second molar of Mestizo and Tarahumara groups (Snyder et al., 1969), and in both teeth in a large Pima sample (Scott et al., 1983). It is noteworthy that in the northern populations, the males show significantly greater fourth-cusp reduction, while in the southern groups, the females display this tendency. No significant dimorphism has been found for third molar hypocone-class proportions; e.g. among Arctic samples, Jomon dentitions, living Australoids and Alaskan Eskimos (Turner, 1967b:58-60; 1979; Bailit et al., 1968; Bang and Hasund, 1973).

In light of the above, it appears that the hypocone-reduction trait is not sex-linked. Turner (1967b:60-61; 1969a) proposed that a model of two codominant autosomal alleles could explain the observed class-frequency distribution (for M^2 and M^3), assuming the Hardy-Weinberg equilibrium was in effect. The predicted results fitted the data from his pooled-Arctic samples and a Peruvian cranial series (Winton, 1966), and also that from living and skeletal Hopi and skeletal (but not living) Koniag populations.

However, this paradigm has not survived further scrutiny. Sofaer (1970) pointed out that the assumption of Hardy-Weinberg equilibrium was not valid in the aforementioned studies, and Lee and Goose (1972) found that Turner's model was not compatible with information drawn from the genetic pedigrees of their Liverpool Chinese groups. The current consensus is that fourth-cusp diminution (a quasicontinuous character) has a polygenic mode of inheritance (Scott and Dahlberg, 1982; Scott et al., 1983; Turner, 1985).

6.2.4 Anatomical description and phylogeny of the distal tubercle character.

The assessment of hypocone reduction is complicated by the occurrence of supernumerary elements on the occlusal surface of the upper molars (see Figure 15a,b, pp. 157-158). The most important of these is the distal tubercle or "fifth cusp"; this occurs on the distal aspect of the metacone (from which it apparently arises), adjacent to the hypocone (Harris and Bailit, 1980). The tubercle varies from a rather minor element, which has little effect on hypocone size, to the small cusp form, that deflects the distal marginal groove markedly toward the lingual, thereby reducing hypocone bulk.

The distal tubercle has a long history within the anthropoid suborder, and apparently occurs in some fossil and living non-hominid anthropoids, e.g. dryopithecines, ramapithecines, cebids, gibbons (Gregory, 1922:455; Harris and Bailit, 1980). In regard to extinct hominids, the fifth cusp has been observed in gracile and robust South African australopithecines (Robinson, 1956:83,89,97), Oriental pithecanthropines and European neantherthals (Weidenreich, 1937b: Plates 15-16). In australo-pithecines, the tubercle tends to increase in frequency and size from the anterior

Figure 15a. Accessory occlusal elements of maxillary molars: distal tubercle and other extra cusps. **(Adapted from Turner, 1967b:97, Figure 9.)**

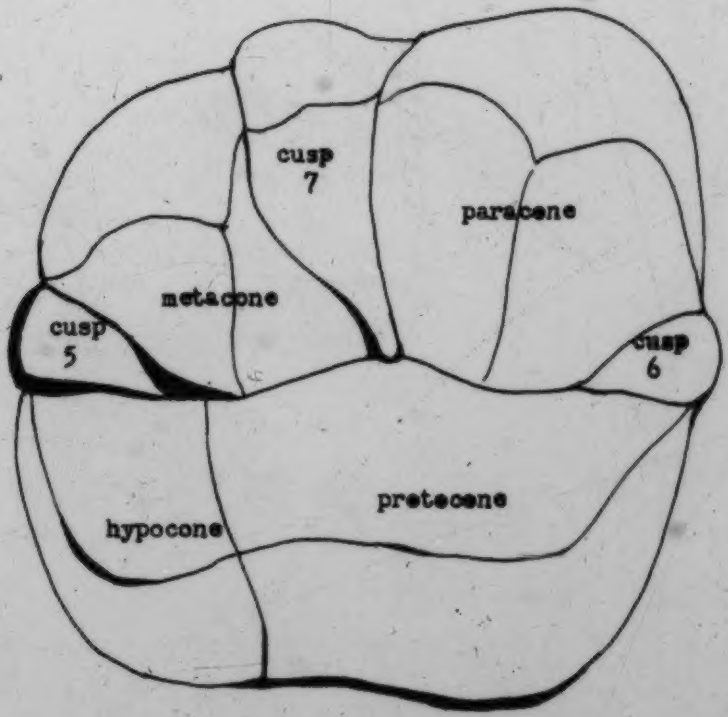
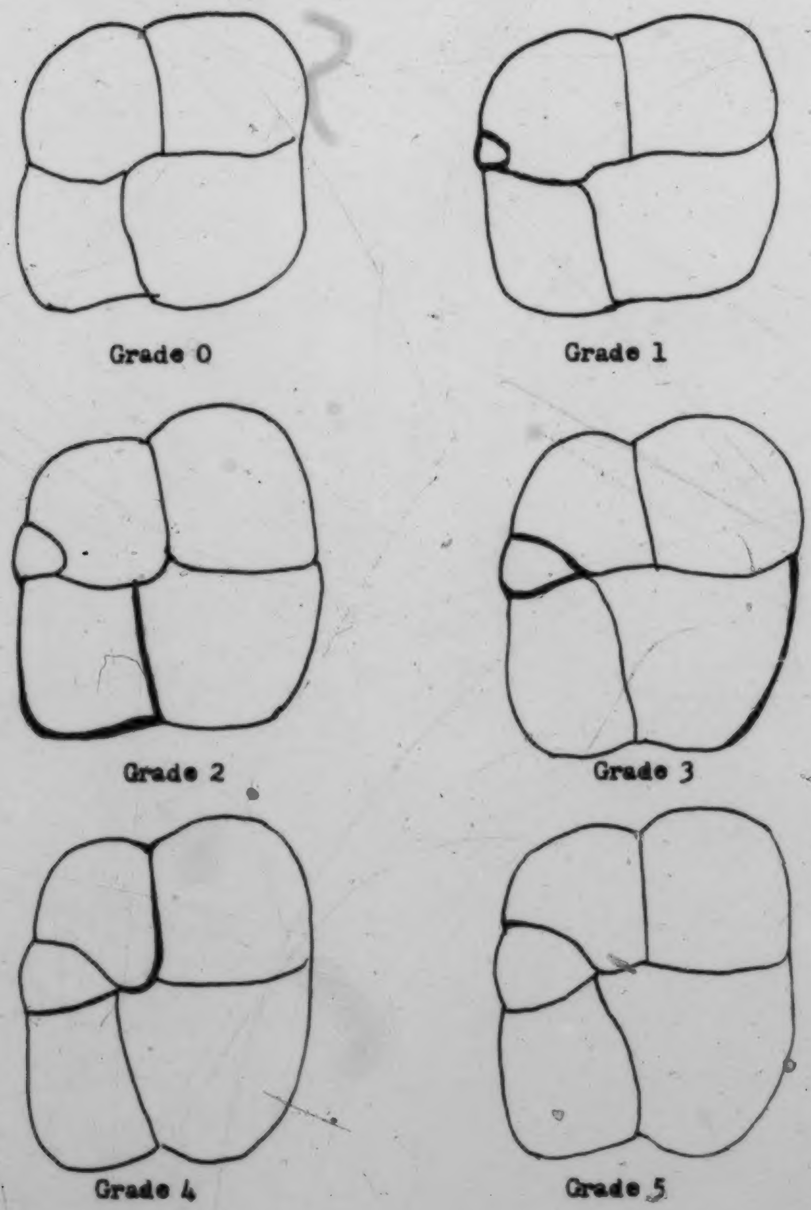

cusp 7
paracone
metacone
cusp 5
cusp 6
hypocone
protocone

Figure 15b. Accessory occlusal elements of maxillary molars: distal tubercle variation. (**Adapted from** Harris and Bailit, 1980: 351, Figure 1.)



Grade 0

Grade 1

Grade 2

Grade 3

Grade 4

Grade 5

molar to the posterior one, and may reach the bulk of the metacone and hypocone in the latter tooth (Robinson, 1956:89-91,94,97).

The modern human pattern of fifth cusp variation is somewhat different from that of the australopithecines. Studies of large samples have demonstrated that the first molar generally displays the highest incidence of the character, while the second molar exhibits the lowest (Harris and Bailit, 1980). The average size of the distal tubercle increases from the anterior molar to the posterior one, but it only rarely equals the hypocone in bulk. In the first two molars, the weakest grade is generally observed (Ibid.; Scott et al., 1983); in the last tooth, a slightly stronger manifestation, viz. grade 2, usually occurs (see Figure 15b, p. 158). Variability in the degree of expression also increases markedly from front to back (Harris and Bailit, 1980).

6.2.5 Racial and geographic variation of the distal tubercle character.

Investigations conducted on small or medium-sized samples have sometimes produced observations conflicting with the general incidence pattern given above. For example, the highest distal tubercle frequency was found on the third molar in Pecos Pueblo crania (Nelson, 1938), Aleut and Arctic Coast Eskimo groups (Turner, 1967b:102), and Melanesian Nasioi and Simeku populations (Harris and Bailit, 1980). The fifth cusp was most often seen on the second molar (and least often on M^1) in one Athapascan sample. However, west Greenland Eskimo and Jomon groups displayed the "typical" pattern (Turner, 1967b:102; 1979).

Distal tubercle frequencies for living populations have only been determined in the last two decades; often, only the first molar incidence is given, e.g. Scott and Dahlberg (1982); Turner (1983; 1985; 1987). However, the use of different scoring procedures by different workers does not allow close (grade by grade) comparisons of the various studies. On a simple presence-absence basis, Melanesian and southern Oriental samples appear to have the highest (M^1) fifth cusp proportions (ca. 30% - 50%); those for northern Oriental and Eskimoid groups tend to be much lower (ca. 10% - 30%). Amerindian populations display the widest range (ca. 5% - 30%) of distal tubercle incidence (Turner, 1979; 1983; 1985; 1987; Harris and Bailit, 1980; Scott and Dahlberg, 1982; Scott et al., 1983). The fifth cusp trait seems to be most useful for micro-geographic sample analyses and comparisons (Harris and Bailit, 1980).

6.2.6 Lateral asymmetry and genetic aspects of the distal tubercle character.

In regard to the distal tubercle expression, the first molar shows the strongest hereditary influence (estimated at ca. 65%) and the lowest environmental influence, which makes it the most suitable one for the determination of frequencies to be used in interpopulation comparisons (Harris and Bailit, 1980). This tooth generally exhibits the highest incidence and the least variation of the fifth cusp, and has the largest "additive genetic component" derivable from fifth cusp proportions. Also, the lateral asymmetry for distal tubercle expression trait is distinctly lower for the anterior molar (16%) than for the other two (24% and 29% for M^2 and M^3, respectively).

Different studies give conflicting evidence concerning the occurrence of sexual dimorphism in distal tubercle frequencies. Significant male-female differences have not been found for any of the three molars in pooled Arctic samples or Japanese Jomon crania (Turner, 1967b:98; 1979). The same result has been given for the two anterior molars (M^1 and M^2) in several American Southwest tribes and also in a large Pima population (Scott, 1973:56-57; Scott and Dahlberg, 1982; Scott et al., 1983).

However, Harris and Bailit (1980) found significant sexual dimorphism in all five of their Melanesian samples (for one or more of M^1, M^2 and M^3), which were larger than most of the populations examined by Scott and Turner. The females generally displayed the higher total trait incidence and individual grade incidence. The possibility that fifth cusp expression is related to the X chromosome is further strengthened by the relatively high heritability estimate derived from female sib data. While autosomal inheritance is therefore uncertain, most workers agree that the distal tubercle character is a quasicontinuous trait with a polygenic mode of inheritance (Harris and Bailit, 1980; Scott et al., 1983; Turner, 1985).

6.2.7 Methodology for occlusal surface features.

In scoring hypocone expression, Dahlberg's (1951) four-grade scale was followed (see Figure 14b, p. 146), as this was the standard used by P.J. Wright (1974:26-27,78,80) and K.E. Wright (1977:18,36,38). A more precise six-class system has been proposed by Scott (1973:29-30) and accepted by some workers (e.g. Turner, 1979; 1983; 1985; Scott et al., 1983), but this could not be used here, as the corresponding plaster plaque was not available at the University of Alberta. While Dahlberg's (1956) plaques P#9 and P#11 could not be obtained either, it was felt that specimen casts approximately matching his (1951, Figure 6) illustrations would suffice for the purposes of standardization in this thesis.

Three additional categories (4+, 2/1, miscellaneous) were introduced to accommodate variation resulting from supernumerary occlusal elements, hypotrophy and unusual form. The 4+ class included molars of regular occlusal type, which manifested a fifth cusp of "moderate" or "large" size, i.e. grades 3-5 (see Figure 15b, p. 158). Distal tubercles of small size, i.e. grades 1-2, were simply ignored when scoring for occlusal pattern. Irregular molars with four or five occlusal convexities were placed in the miscellaneous category; the 3++ type (cuspule-hypocone form with prominent fifth element was considered a "4+" expression. Greatly reduced teeth (e.g. bicuspid and peg elements were assigned to the 2/1 class (see Figure 14c, p. 147).

K.E. Wright (1977:18,36,38) also used extra grades (i.e. 4+/5, 2+, 2) to describe observed upper molar variation. P.J. Wright (1974:26-27,78-81) apparently did not find unusual types in any of his three Iroquoian samples. While the first author considered all three molars, the second excluded the posterior tooth from his study.

In this thesis, all three molars were examined and observations taken on both sides of each cast, so that side and individual counts could be made. In cases of lateral grade asymmetry (for the individual count), the specimen was assigned to the higher class. When one antimere displayed an unusual occlusal pattern, and the other a regular type, the individual was placed in the miscellaneous category.

The distal tubercle was scored according to Harris and Bailit's (1980) six-class scale (see Figure 15b, p. 158), except that the weaker expressions (grades 1-2) were lumped together, as were the moderate manifestations (grades 3-4), because of the difficulty experienced in placing several of these elements strictly into one category with confidence. Harris and Bailit's standard has also been accepted by Scott et al. (1983). Scott (1973:31) used a four-class scheme, but this did not encompass the full range of fifth cusp variation. Turner (1983; 1985; 1987) has also followed a six-grade system, but has not defined this in the available literature. K.E. Wright (1977:18,36-39) did not specifically investigate distal tubercle expression; P.J. Wright (1974:26-27,78-81) gave statistics for the "distal marginal tubercle", but the relationship of this feature to the fifth cusp is uncertain.

Observations were also made on two other supernumerary occlusal elements which occasionally occur on the maxillary molars: the mesial "sixth cusp" and the mediobuccal "seventh cusp" (see Figure 15a, p. 157). Turner's (1967b:96-97, Figure 10) designation of the former is accepted here. However, the nature of his "seventh cusp" is not clear from his diagram. It appears to be an occlusal element, but is referred to in the text as a facial or paramolar entity. As the mediobuccal position is not the most common one for a paramolar tubercle (Bolk, 1916; Pedersen, 1949:134-136; Kustaloglu, 1962), the term "seventh cusp" will be used to label the mediobuccal occlusal element sometimes observed in this study of Iroquoian teeth.

6.2.8 Observations on occlusal surface features.

The general trend of hypocone reduction from anterior to posterior molar was reflected in the upper teeth of the Grimsby sample (see Tables 10a,10b, pp. 165-167). The first molars fell within the 4 or 4- categories (56.7% and 41.7%, respectively; n = 60) with a single (4+) exception. The second molars usually displayed the 4- pattern (70.9%, n = 55), but a notable proportion (18.2%) were of the 3+ type. Among the third molars, the 3+ and 3 groups formed the largest classes (31.7% and 39.0%, respectively; n = 41).

The third molars had the most diverse occlusal morphology, which ranged from the 4- pattern (in two individuals) to the unicuspid or peg type (in 3 specimens). There was also a notable incidence of irregular four or five cusped elements (14.6%). In one indeterminable case (Fe 9#9), the left bicuspid antimere resembled a "giant" cylindrical peg, while the right had a regular but diminished tricuspid form.

The peg-tooth anomaly may be affected by sexual dimorphism. The three specimens in the observed sample with peg teeth were Fe1#27 (female, M^3), Fe20#1 (male, RM^3), and Fe27#3 (male, RM^3). Jackes (in press) noted the occurrence of a fourth (noncasted) example in the Grimsby crania (Fe17#1, male, LM^3). Except for Fe1#27, the opposing (M^3) antimere was not present in any of the above cases.

TABLE 10a. OCCLUSAL SURFACE PATTERNS OF MAXILLARY MOLARS IN THE GRIMSBY SAMPLE: OCCURRENCE BY SIDE.

	FIRST MOLAR		SECOND MOLAR		THIRD MOLAR	
	L SIDE	R SIDE	L SIDE	R SIDE	L SIDE	R SIDE
SEX	#	#	#	#	#	#
MALE						
4+	0	0	0	0	0	0
4	13	11	0	1	0	0
4-	12	12	17	19	2	0
3+	0	0	5	4	4	3
3/2+	0	0	0	0	8	6
2/1	0	0	0	0	0	3
misc.	0	0	1	1	1	2
total	25	23	23	25	15	14
FEMALE						
4+	1	1	3*	2*	0	0
4	12	11	0	0	0	0
4-	8	10	9	14	0	0
3+	0	0	7	6	7	5
3/2+	0	0	0	0	4	3
2/1	0	0	0	0	1	2
misc.	0	0	0	1	3	3
total	21	22	19	23	15	13
ALL						
4+	1	1	3*	2*	0	0
4	30	27	30	37	2	0
4-	24	27	30	37	2	0
3+	0	0	13	11	11	8
3/2+	0	0	0	0	12	12
2/1	0	0	0	0	2	5
misc.	0	0	1	2	4	5
total	55	55	47	53	31	30

*Specimens with 3++ pattern included in figure.

TABLE 10b. OCCLUSAL SURFACE PATTERNS OF MAXILLARY MOLARS IN THE GRIMSBY SAMPLE: OCCURRENCE BY INDIVIDUAL.

SEX	FIRST MOLAR INDIVIDUAL # (%)	SECOND MOLAR INDIVIDUAL # (%)	THIRD MOLAR INDIVIDUAL # (%)
MALE			
4+	0 (0.0)	0 (0.0)	0 (0.0)
4	15 (57.7)	1 (3.8)	0 (0.0)
4-	11 (42.3)	20 (76.9)	2 (10.5)
3+	0 (0.0)	4 (15.4)	5 (26.3)
3/2+	0 (0.0)	0 (0.0)	8 (42.1)
2/1	0 (0.0)	0 (0.0)	2 (10.5)
misc.	0 (0.0)	1 (3.8)	2 (10.5)
total	26 (100)	26 (100)	19 (100)
asym.	3/26	1/26	1/19
FEMALE			
4+	1 (4.2)	3 (12.5)*	0 (0.0)
4	14 (58.3)	0 (0.0)	0 (0.0)
4-	9 (37.5)	15 (62.5)	0 (0.0)
3+	0 (0.0)	5 (20.8)	8 (42.1)
3/2+	0 (0.0)	0 (0.0)	5 (26.3)
2/1	0 (0.0)	0 (0.0)	2 (10.5)
misc.	0 (0.0)	1 (4.2)	4 (21.1)
total	24 (100)	24 (100)	19 (100)
asym.	1/24	3/24	2/19
ALL			
4+	1 (1.7)	3 (5.5)*	0 (0.0)
4	34 (56.7)	1 (1.8)	0 (0.0)
4-	25 (41.7)	39 (70.9)	2 (4.9)
3+	0 (0.0)	10 (18.2)	13 (31.7)
3/2+	0 (0.0)	0 (0.0)	16 (39.0)
2/1	0 (0.0)	0 (0.0)	4 (9.8)
misc.	0 (0.0)	2 (3.6)	6 (14.6)
total	60 (100)	55 (100)	41 (100)
asym.	4/60	4/55	4/41

*Specimens with 3++ pattern included in figure.

While the first molars exhibited no unusual occlusal variations (0%, n = 60), irregular teeth were found among the second molars (7.3%, n = 55) and especially, the third ones (14.6%, n = 41). The 3++ type was only manifested by the second molars (bilaterally, with medium-sized distal tubercles) in two female individuals (3.6%, n = 55). Several aberrant forms occurred only among the last molars. In terms of cusp number, these could be classified into the 4+, 4, 3++ and 3 grades, but all displayed unusual cusp proportions and groove configurations (e.g. a few resembled the mandibular "Y4" and "X4" patterns).

The seventh cusp was observed in only three specimens, two males (Fe52#1, Fe62#82) and one female (Fe46#1). It occurred bilaterally, in low frequencies, on both the middle molar (3.6%, n = 55) and the posterior tooth (2.4%, n = 41), and was always much smaller than the protocone and paracone. In all cases, both metacone and hypocone were reduced in size, with the latter taking the form of a cuspule.

Only slight differences in male and female grade frequencies were observed for hypocone expression; there was no good evidence for sexual dimorphism in this trait for the Grimsby population. The males showed a somewhat greater reduction in the anterior molar, and the females in the two posterior teeth (for the standard classes). However, male individuals displayed greatly reduced bicuspid, near-bicuspid or unicuspid third molars (on one or both sides) twice as often as female individuals (i.e. six cases to three cases).

The genetic instability of the third molar was reflected in the frequencies of lateral grade asymmetry (6.7%, n = 60 for M^1; 7.3%, n = 55 for M^2; and 14.6%, n = 41 for M^3), but the probability values for the differences between the molars were no significant. Asymmetry was always of the 4/4- kind in the first molar and the 4-/3+ pattern in the second. In the last molar, standard-grade asymmetry took the form of a tricuspid or near-tricuspid element (3/3+) on one side and a bicuspid or near-bicuspid tooth (2/2+) on the other (9.8%, n = 41). There were also a couple of female specimens (4.9%) which displayed one regular antimere (3+/3) and one aberrant type (3+/3++ cusp number).

The pattern of distal tubercle frequencies was rather unusual (see Table 11, p. 170), in that the second molar had the highest incidence (13.0%, n = 46), followed by the first and last ones (7.8%, n = 51 and 5.1%, n = 39, respectively). The middle molar also had the highest proportion of large (2.2%) and moderate (4.3%) fifth cusp classes. The cuspule type was the dominant manifestation of the metaconule in all three molars. The fifth cusp was expressed bilaterally in all determinable cases of occurrence; female individuals generally displayed a higher

TABLE 11. DISTAL TUBERCLE CHARACTER OF MAXILLARY MOLARS IN THE GRIMSBY SAMPLE: OCCURRENCE BY INDIVIDUAL.

SEX	FIRST MOLAR		SECOND MOLAR		THIRD MOLAR	
	#	(%)	#	(%)	#	(%)
MALE						
0	18	(90.0)	19	(95.0)	18	(100)
1-2	2	(10.0)	1	(5.0)	0	(0.0)
3-4	0	(0.0)	0	(0.0)	0	(0.0)
5	0	(0.0)	0	(0.0)	0	(0.0)
total	20	(100)	20	(100)	18	(100)
asym.	0/2		0/1		0/0	
FEMALE						
0	19	(90.5)	16	(76.2)	16	(88.9)
1-2	1	(4.8)	2	(9.5)	2*	(11.1)
3-4	0	(0.0)	2	(9.5)	0	(0.0)
5	1	(4.8)	1	(4.8)	0	(0.0)
1-5 (to.)	2	(9.5)	5	(23.8)	2*	(11.1)
total	21	(100)	21	(100)	18	(100)
asym.	0/2		0/5		0/2	
ALL						
0	47	(92.2)	40	(87.0)	37	(94.9)
1-2	3	(5.9)	3	(6.5)	2*	(5.1)
3-4	0	(0.0)	2	(4.3)	0	(0.0)
5	1	(2.0)	1	(2.2)	0	(0.0)
1-5 (to.)	4	(7.8)	6	(13.0)	2*	(5.1)
total	51	(100)	46	(100)	39	(100)
asym.	0/4		0/6		0/2	

*Specimens with irregular occlusal surface patterns present.

incidence of the feature, but sample size was rather small for testing the significance of sexual differences.

The fifth cusps characteristically found in the 3++ second molar specimens did not occur in the typical distal tubercle position. In one individual (Fel#17), the left element exhibited a fifth cusp which was lingual (rather than buccal) to the distal marginal groove, so that with the diminished fourth cusp, the impression of a "split-hypocone" was produced. However, the right tooth displayed a distal tubercle of the same size in the normal situation. In the other case (Fe9#45), both antimeres showed the "split-hypocone" expression. It is possible that this unusual "fifth cusp" manifestation represents a different character than the distal tubercle character; however, the example of cast Fel#17 would argue otherwise, and the "split-hypocone" pattern is accepted here as a distal tubercle variation.

The mesial sixth cusp was always a very minor element in the occlusal surface, and was usually bilaterally expressed. There was one case observed for the first molar, three cases for the second, and four for the third. It would appear that sixth cusp frequency increases along an anterior to posterior gradient; however, because of its rather small size and the high probability of eradiction by even slight wear, accurate proportions (and lateral asymmetry percentages) cannot be given with confidence for this feature.

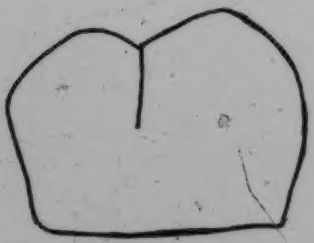
6.3 Carabelli trait of the maxillary molars.

6.3.1 Anatomical description and phylogeny of Carabelli trait.

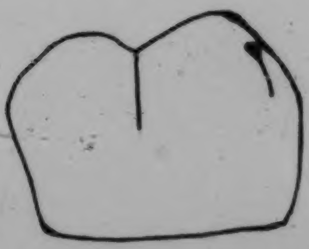
The Carabelli trait has been known, in one form or another, for more than 150 years, and is probably the single most studied dental character (Korenhof, 1960:251, 257). The cusplike expression was first noted by Rousseau in 1827, but the type description was given by Carabelli in 1842 (cited by Korenhof, 1960:251). The feature described was a prominent "free-standing" tubercle (with a distinct furrow), invariably situated on the lingual surface of the protocone of the upper molars (Jørgensen, 1956:132-133; Korenhof, 1960:253-254). However, by the end of the late nineteenth century, it had become apparent that this compound "positive" structure could be associated with simple "negative" structures, i.e. grooves or pits, which occurred in the same place (Black, 1890:61; 1897:63; Batujeff, 1896).

As implied above, the Carabelli trait is extremely variable in its phenotypic character (see Figures 16a,16b, pp. 173-174). Negative expressions take the form of single or double grooves, furrows or pits of different shapes. Positive structures range from a distinct swelling or bulge of extra tooth substance which lacks clearly-defined delimiting furrows to a cusplike eminence with a fused apex to a large and more or less "free" tubercle; single or double vertical ridges may also be included here (Kraus, 1959; Dahlberg, 1963a; Kirveskari, 1974:36-37; Scott, 1980;

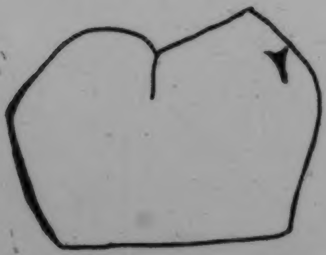
Figure 16a. Carabelli trait of maxillary molars: negative expressions.



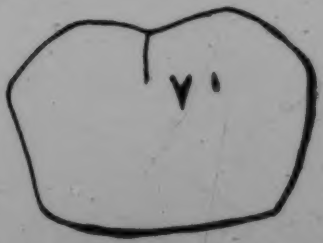
Grade 0
(trait absence)



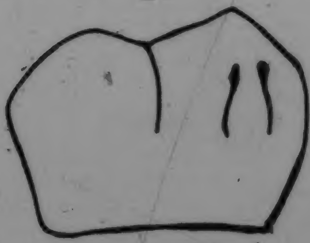
Grade 1
(groove with small pit)



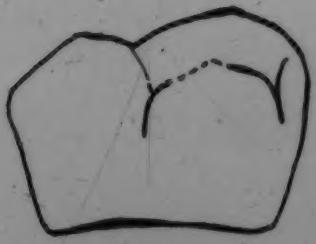
Grade 2
(pit)



Grade 2
(2 pits)

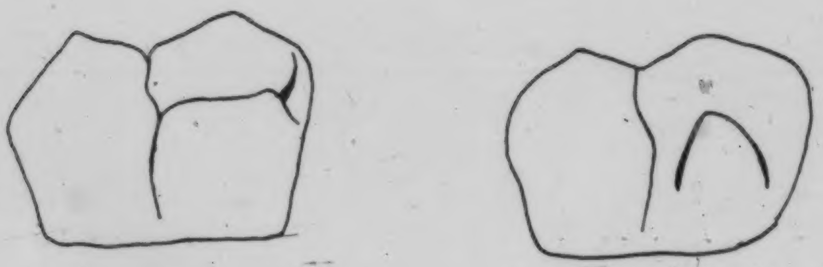


Grade 3
(2 grooves)



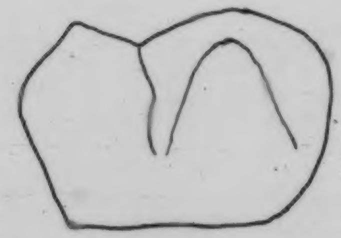
Grade 4
(Y-groove)

Figure 16b. Carabelli trait of maxillary molars: positive expressions.



Grade 5
(small tubercle)

Grade 5
(small tubercle)



Grade 6
("cusp outline")

Mayhall et al., 1982). The weakest expression may be described as a vertical ridge (Dietz, 1944) or a furrow (Kraus, 1951) or a combined ridge and furrow (Scott, 1980). The strongest Carabelli manifestation is a prominent tubercle, which may reach or even exceed the size of the major occlusal cusps (Zeisz and Nuckolls, 1949:193; Kraus et al., 1969:87,296; Kirveskari, 1974:34,37).

It is now generally accepted that the Carabelli character originates in the lingual cingulum (Kirveskari, 1974:34; Scott, 1980; Sakai, 1982; Scott et al., 1983). Decisive influences in this regard have been Korenhof's (1960:301-303, 307) study of molar endocasts and (especially) Kraus' investigations into dental embryology (Kraus and Jordan, 1965:178-189; Kraus et al., 1969:297-298). The former showed that the weaker enamel cusplike structure often corresponded to a cingular dentine swelling or cingular dentine remnant; the latter demonstrated that positive Carabelli manifestations arise out of the "developmental cingulum" and that negative ones only occur in the absence of this dental zone. It might be noted that many of the earlier workers also associated the Carabelli trait with the lingual cingulum (e.g. Windle and Humphrey, 1887; Cope, 1889).

There has been some discussion on the nature of the grooves observed on the lingual protoconal surface (see Figure 16a, p. 173). It is generally agreed that the single

"Carabelli groove" found in the mesiolingual region represents the mesial portion of the Carabelli furrow, which when fully developed takes on a characteristic semicircular shape and separates the Carabelli tubercle from the protocone (Shapiro, 1949; Korenhof, 1960:255-256,287; Kirveskari, 1974:36). In the case of the double-groove form, or "negative cusp-outline", the distal fissure represents the distal portion of the Carabelli furrow (Shapiro, 1949; Kirveskari, 1974:36).

The "Y-shaped furrow" (which sometimes lacks the stem portion) has a mesial and a distal branch, the latter being associated with the single Carabelli groove (Korenhof, 1960:287-288, 306; Kirveskari, 1974:36). The mesial arm has been identified with Korenhof's (1960:256, 288, 307) "cingulum groove", which arises from the mesiolingual cingulum and is oriented in a mesio-occlusal direction. Jørgensen (1956:133-134) referred to the same negative structure as the "protoconule groove"; however, the name is not valid because of the great improbability that a protoconule remnant exists in modern man (Korenhof, 1960:256).

The occurrence of a third "occlusal groove" in the same general mesiolingual area as the other two has resulted in some confusion and disagreement. This groove courses over the mesial marginal ridge, in a mesiolingual direction, onto the mesial protoconal surface (Snyder et al., 1969).

Kirveskari (1974:34,36) identified the cingulum groove with the mesiolingual occlusal groove, as well as with the mesial branch of the Y-shaped furrow.

However, Korenhof (1960:287-288) remarked that the cingulum groove does not reach the occlusal plane, except in molars showing some degree of attrition. Furthermore, the mesial arm of the Y-shaped furrow clearly does not reach the mesio-occlusal border in illustrations given for this manifestation (e.g. Korenhof, 1960:283; Dahlberg, 1963a; Turner, 1967b:67, Figure 7; Scott, 1980: Figure 1). It appears, then, that the cingulum groove is a separate entity from the occlusal groove.

A Carabelli pit generally takes the form of a distinct and relatively deep round or ovoid enamel indentation, which may occur at two loci in the central third of the lingual protoconal surface (Turner, 1967b:67, Figure 7; Kirveskari, 1974:37). The mesial pit is supposedly manifested at the site where the cingulum groove would meet the Carabelli furrow, and may occur together with the Carabelli groove (Jørgensen, 1956:134; Korenhof, 1960:255-256). The distal pit apparently marks the distal portion of the fully-developed furrow (Korenhof, 1960:306-307).

In addition to the pit form, less pronounced negative structures are also found associated with the Carabelli trait (see Figure 16a, p. 173). A weak, triangular depression can occur in the crotch of the Y-shaped furrow (Korenhof, 1960:288; Kirveskari, 1974:36). A similar shallow indentation is occasionally seen at the occlusal end of the cingulum groove, and may represent the last trace of that groove when it appears without the latter (Korenhof, 1960:288-289, Plate 17, Figures 10-11 and Plate 10, Figure 3). Also, a distinct subocclusal pit, possibly marking the "crest" of the Carabelli furrow, is sometimes observed on the lingual protoconal face (Shapiro, 1949). These slighter manifestations have been confused, in a few cases, with the Carabelli pit as defined above.

Investigations into the internal anatomy and ontogeny of the upper molars have supported the belief that negative Carabelli structures and positive ones belong to the same trait complex, an assumption which has been disputed by Dahlberg (1951), Kallay (1957; 1966) and Hanihara (1963). Carabelli invaginations (grooves and pits) occurring in the enamel surface of a tooth, without an associated cusplike eminence, are only rarely reflected in the dentine topography of the same element. Instead, the endocast generally shows a cervical convexity, i.e. a distinct "dentine cingulum" (Korenhof, 1960:303, 305). Dentine pits appear only in the absence of the "developmental cingulum" at the Carabelli site, during the early calcification phase. Indentations at the same locus have been observed even in the late precalcification period, and it is notable that bulges representing the tubercle at this locus can be manifested at an equally early embryological stage (Kraus and Jordan, 1965:188-189; Kraus et al., 1969:297-298).

A positive Carabelli structure represents a buildup of enamel and dentine. Korenhof (1960:301-303) has demonstrated that endocasts of most molars with sizable external tubercles show cusps on the dentine surface as well, which are proportionately as large as the overlying enamel convexities. In the case of a small, weakly-defined protuberance, the corresponding internal manifestation is simply a dentine swelling of the cingulum. In specimens displaying a prominent tubercle with a fused apex, the endocast exhibits a slightly grooved eminence or at least a cingular remnant. There is also some evidence that pulp material may compose part of the cusp formation (Odio de Granda, 1927; Kallay, 1957; 1966; Korenhof, 1960:262).

There has been some disagreement in the literature over the nature of the double groove and Y-shaped furrow variations. In cases where these phenotypes occur, the encircled protoconal area may be slightly protuberant (Kirveskari, 1974:37). However, because these "negative cusp-outlines" are indentations in the normally convex lingual surface, a supposed prominence may be more apparent than real. A number of workers have considered the double groove or Y-shaped furrow or both to be tubercular forms, e.g. Suzuki and Sakai (1957); Tsuji (1958); Dahlberg (1963a) and Garn et al. (1966c); and also, seemingly, Moorrees

(1957:39), Snyder et al. (1969), and Beynon (1971). However, the tendency in recent years has been to include these two groove types in the general category of negative expressions (e.g. Kirveskari, 1974:36-37; Alvesalo et al., 1975; Scott, 1980; Kieser, 1984a,b), a procedure which will be followed here.

The expression of the Carabelli feature assumes a characteristic pattern in modern individuals. The first molar usually displays the strongest form of the trait, while the second and third molars tend to show progressively weaker manifestations or none at all (Windle and Humphreys, 1887; Zeisz and Nuckolls, 1949:192; Dahlberg, 1951; Moorrees, 1957:36). This is partly reflected in the class incidence distributions for a number of populations; the largest proportions of the cusplike phenotype are found on the anterior molar and the lowest (generally) on the posterior one (Dahlberg, 1963a; Mayhall, 1979b; Mayhall et al., 1982).

The highest incidence of the Carabelli trait is invariably found on the anterior molar (Korenhof, 1960:298), while the lowest incidence is most often found on the posterior one (Kraus, 1951; Lasker and Lee, 1957; Moorrees, 1957:36). This pattern has been observed for a number of populations, e.g., South African Bantu and Bushmen (Shapiro, 1949); East Greenland Eskimos (Pedersen, 1949:98-99); central Arctic Eskimos (Mayhall, 1979b); Indian Knoll

Amerindians (Dahlberg, 1951); Pimas (Dahlberg, 1963a); Chicago whites (Dahlberg, 1963a); Burlington white children (Saunders and Mayhall, 1982) and a mixed American (Negroid and Caucasoid) sample (Dietz, 1944). In a few cases, e.g. a hybrid Eskimo-white series (Pedersen, 1949:99) and a Burlington Euro-American (adult) group (Mayhall et al., 1982), where sides or teeth (rather than individuals) were counted the third molar trait frequency was slightly higher than that of the second element.

One remarkable exception to the general tendency is found in Turner's (1979) study of the Jomon dentition, where the third molar displays the most pronounced manifestation and the second highest proportion(about three times the M^2 incidence) of the Carabelli trait. The grade frequency pattern for this tooth is rather aberrant. Only the strongest ("high cone") and weakest ("furrow") expressions were observed, and the former occurred three times as often as the latter.

It seems likely that Turner's "high cone" represents the fortuitous "entomolar" cusp which is sometimes found at the Carabelli locus on the last molar (see Subsection 6.4.1, pp. 207-216). This variation has a fused or separate root element; occasionally, two small tubercles are seen instead of one large eminence. The entomolar protuberance may belong to the Carabelli complex, but most workers consider it to be a separate character (Turner, 1967b:96-98; Taylor, 1978:252-253,275-285,334-335).

The pattern of Carabelli phenotypes displayed by the oldest hominids is apparently the reverse of that seen in modern man. Trait expression is most frequent and most pronounced on the third molar, and the least frequent and weakest on the first one (Sperber, 1975:66-67,78,93-94). Carabelli manifestations were generally stronger in the earlier, gracile australopithecine (at Sterkfontein) than in the later robust type (Swartkrans); some specimens of the former exhibit a tubercle as much as 2.5 mm. wide on the last molar. This tendency has been suggested by at least two major works on australopithecine dental morphology (Ibid.; Robinson, 1956:82-86,89-91,94-96).

The Carabelli feature has been observed in fossil hominie dentitions, but the evidence is scarce and its interpretation affected by the possibility of marked geographic variation (Jørgensen, 1956:132-133). Oriental pithecanthropines rarely show the trait and weaker expressions are usually seen, e.g. pits and grooves, although one specimen from Java displayed a prominent tubercle (Weidenreich, 1937a:75,166; Korenhof, 1960:295-297). The Mousterian and Krapina neanderthals mainly exhibited negative phenotypes, e.g. small pits and grooves (Adloff, 1907; Gorjanovic-Kramberger, 1907; Gregory, 1922:454). Claims of cusplike eminences on the Krapna dental elements are controversial (Weidenreich, 1937a:75; Jørgensen, 1956:135), although Korenhof (1960:297) noted the presence of at least one distinct tubercle. The modern pattern of Carabelli phenotypes may have occurred in the Krapina population; the trait is manifested on all determinable first molars, but is less frequent on the other posterior teeth.

The Carabelli trait has an ancient and widespread history within the primate order. The cusp form or "protostyle" (Osborn, 1907:158-159) occurs in two Eocene ~~tarsioids~~ tarsoids (Jorgensen, 1956:120; Sakai, 1982), as well as in recent lemurs and other prosimians (Cope, 1889; Odio de Granda, 1927; Weidenreich, 1937a:74,76; Kirveskari, 1974:35). Negative phenotypes are also found in fossil and extant prosimians (Weidenreich, 1937a:77; Korenhof, 1960:263-265). Extinct catarrhines (e.g. Pliopithecus) display mesial grooves (Korenhof, 1960:266) while living baboons and other cercopithecid monkeys occasionally exhibit a pronounced eminence (Batujeff, 1896; Odio de Granda, 1927).

Tubercles are seldom seen in modern gibbons and the great apes (Gregory, 1922:377,454; Weidenreich, 1937a:76). According to Korenhof's (1960:279-280, 283-284) data, frequencies are 3.0% for the gorilla, 0.6% for the chimp and 0.0% - 2.3% for the orang. Negative phenotypes reach significant proportions only for the orang (ca. 65% - 95%). Pits and furrows (rarely cusps) have been found in the dentitions of Neogene "pongids",, e.g., *Sivapithecus*, *Dryopithecus* and *Gigantopithecus* (Ibid.:267-270,307).

Some workers believe that the stronger Carabelli phenotypes might serve a useful purpose in modern hominids. Schwarz (1927a,b) thought that the cusp-form functioned as an "extra anchorage" in the chewing activities of the first upper and lower molars. This protuberance would fit into the lingual notch between the metaconid and entoconid.

A more widely held theory proposed that the first molar was developing a large tubercle in order to compensate for the loss of occlusal area resulting from the reduction of the other maxillary molars (e.g. Batujeff 1896; de Terra, 1905:162; Hirsch, cited by Korenhof, 1960:259; Brockman, 1938a,b; Dahlberg, 1963a). However, a number of studies have indicated that Carabelli cusp expression and hypocone reduction or absence are opposing tendencies (Jorgensen, 1956:139; Moorrees, 1957:40-41) and statistical tests have demonstrated that a negative association exists between these two characteristics (Keene, 1965; Hanulik et al., 1966; Scott, 1979). It should also be noted that in many cases the masticatory advantage gained by a large Carabelli element is offset by a diminished protocone (Dahlberg, 1951; Snell, 1959).

There is evidence, though, that the more prominent Carabelli convexities serve an important function in the chewing activities of some racial groups. A pronounced tubercle reaching or approaching the occlusal surface may be found in notable proportions (ca. 7% - 10%) in European-derived samples and in significant frequencies (ca. 4% - [illegible]) in a few African and Oceanic populations, viz. Bantu, Bushmen, Melanesians, Polynesians (Scott, 1980). It might be noted that the largest molar (M^2) in the gorilla is exposed to the greatest grinding pressure and also most often shows the Carabelli cusp, and that this situation corresponds to that for the first molar in modern man (Korenhof, 1960:309-310).

Begg (1954) demonstrated that an uneven pattern of dental attrition can produce greater lingual wear that may bring a prominent Carabelli protuberance into the occlusal plane, thereby increasing the masticatory surface. Korenhof (1960:300) observed several Malaysian specimens in which this had apparently occurred. Under these conditions, the tubercle will interact with the seventh cusp of the opposing lower molar, when the latter is present, and Barnes (1969) found a significant positive association between these two features (on M^1 and $\underline{M_1}$) among the Ugandan Teso.

6.3.2 Racial and geographic variation of Carabelli trait.

Since the late nineteenth century, dental anatomistis have noted that the Carabelli tubercle was more commonly observed in some racial groups than others (e.g. Batujeff, 1896; de Terra, 1905:157,296). The work of Tratman (1939;

1950a,b) and Pedersen (1949:96-98) was particularly influential in demonstrating that a low Carabelli cusp frequency was characteristic of Asiatic Mongoloid and Eskimoid populations, while a distinctly higher incidence was generally found among Caucasoid peoples (cf. Lasker, 1950; Dahlberg, 1951; Kraus, 1951; Jørgensen, 1956:132; Lasker and Lee, 1957). According to the rare studies done by the earlier authors, Negroid and Australoid samples displayed low and Melanesian samples intermediate proportions for the positive Carabelli expressions (see Pedersen, 1949:96-97; Lasker, 1950; Dahlberg, 1951).

However, studies made by different workers in the late nineteenth and early twentieth centuries are of dubious values for comparative purposes. De Terra (1905:162, Figure 21) apparently confused the Carabelli cusp with the paramolar tubercle (see also Korenhof, 1960:261).. Many of the earlier workers (e.g. Bolk, Campbell, Chiavaro, Hirakawa, Hjelmman, Vram) did not clearly define what they accepted as Carabelli variations (see Pedersen, 1949:96-97; Jorgensen, 1956:137-138; Korenhof, 1960:256; Kirveskari, 1974:38), and neither have some more recent authors (e.g. Lasker, 1950; Moorrees, 1957:38-40; Brabant, 1971).

In some cases classification systems were explicitly outlined, but only a portion of the range of Carabelli expressions might be considered. Nelson (1937), Dahlberg (1951) and Lasker and Lee (1957) only counted distinct cusps, while Suzuki and Sakai (1957), Tsuji (1958), Pinto-Cisternas and Figueroa (1968) and Beynon (1971) ignored single grooves and pits. Barnes (1969) did not include negative phenotypes in his figures for the Carabelli trait; Turner (1983; 1985; 1987) excluded single furrows from his statistics for different populations.

Even when a system adequate for documenting all known forms of the Carabelli trait is used, e.g. Dahlberg's (1963a) scheme, there is still a problem in classifying the degree of expression, especially for the cusplike phenotypes. Korenhof (1960:256) criticized the subjective use of adjectives such as "weak, strong, normal, small, large, etc." to describe the appearance of Carabelli structures. However, this difficulty has been greatly reduced by the widespread use of Dahlberg's (1956) standard plaques, which provide a three-dimensional reference system for classifying Carabelli variations.

It might be noted that Dahlberg's (1963a) scale may not be enough by itself to ensure minimum interobserver error. For instance, Dahlberg (1963a) found an incidence of ca. 90% for the Carabelli trait among a Pima group represented by stone casts, while Sofaer et al. (1972b) gave a frequency of ca. 50% for the same population, using the same material and the same classification scheme (although not the standard plaques). This gross error between the two studies (ca. 40%) was presumably due to the difference in observational experience, especially in regard to the presence of the weakest Carabelli expressions.

Criticisms of the comparability of Carabelli trait proportions presented by different workers have been made by a number of modern authors (e.g. Lasker and Lee, 1957; Kraus, 1959; Korenhof, 1960:308-309; Kraus and Jordan, 1965:178; Turner, 1967b:66; Scott, 1980). Taylor (1978:336) even states that "so-called statistics concerning its occurrence are worthless," because of the subjectivity involved in judging the prominence and nature of the manifestations. However, he apparently believes that the standard plaques are useful for classifying morphological features (Taylor, 1978:338).

Scott (1980) observed that distinctive patterns of Carabelli manifestation were characteristic of different racial groups. He found that both Oceanic (Hawaiian, Melanesian) and Arctic (Aleut-Eskimo) samples showed comparatively low trait frequencies (ca. 44% - 47%), but the former had relatively high frequencies (ca. 16% - 26%) of the cuspoid phenotypes while the latter had extremely low frequencies (ca. 1%). Asio-Indian and Bantu populations exhibited intermediate proportions of total trait manifestation (ca. 62% and ca. 73%, respectively) and tubercular forms (ca. 9% - 12%). Southwestern tribes and Bushmen also displayed intermediate incidences of trait presence (ca. 67% - 70%), but convex structures were rather rare among the former (ca. 5%) and relatively common (ca. 17%) among the latter.

Scott (1980) found that Caucasoid (American, South African) samples showed the highest ~~overall~~ trait frequencies (ca. 75% - 85%) and cusp frequencies (ca. 24% - 33%). Other workers have reported similar results for various European-derived populations, e.g., Ohio whites, Hailuoto Finns, Ontario whites. Total trait proportions ranged from ca. 70% - 90%, and tubercle proportions from ca. 20% - 46% (Garn et al., 1966g; Alvesalo et al., 1975; Mayhall et al., 1982; Saunders and Mayhall, 1982).

Only a few studies have been done on native sub-Saharan peoples. Barnes' (1969) Ugandan Teso displayed an incidence of ca. 10% for convex Carabelli expressions, a figure which approximates that given by Scott (1980) for South African Bantu (ca. 12%). However, Hassanali (1982) presents a much higher cusp-statistic for Kenyan negroes (ca. 23%), although total trait presence among his subjects (ca. 67%) is similar to that manifested by Scott's groups (ca. 73%). It seems likely that cusp frequencies differ markedly among diverse African tribes.

Australoid populations apparently exhibit the greatest variation in Carabelli phenotypes. Studies of several groups indicate that overall trait proportions range from ca. 42% - 90% and tubercle proportions, from 0% - 27%. There also seems to be a gradient of trait expression, with the inland tribes showing higher frequencies (ca. 70% - 90%) than the coastal tribes (Richards and Telfer, 1979; Townsend and Brown, 1981).

Mongoloid groups are characterized by a relatively low incidence (ca. 0% - 5%) of the convex Carabelli phenotypes, confirming the earlier conclusions of Pedersen (1949:96-98) and Tratman (1950a,b). Arctic samples (e.g. Aleut-Eskimo and Athapascan) and Southeast Asian peoples (e.g. Japanese Jomon) also have low total trait frequencies of ca. 20% - 50% (Turner, 1967b:69,75; 1979; Scott, 1980). American Southwest tribes generally have intermediate total trait frequencies, ranging from a low of ca. 58% for the Athapascan-derived Apache to a high of ca. 80% for the Hopi (Scott and Dahlberg, 1982; Scott et al., 1983).

Snyder et al. (1969) have reported a couple of possible exceptions to this general pattern. The Tarahumara and hybrid Mestizo of northwestern Mexico show extremely high incidences for protuberant phenotypes (ca. 61% - 63%) and total trait presence (ca. 95% - 98%). However, it is likely that Snyder and his co-workers included negative cusp-outlines in their counts of tubercular manifestations (cf. Dahlberg, 1963a).

6.3.3 Lateral asymmetry and genetic aspects of Carabelli trait.

The first worker to regard the Carabelli cusp as hereditary (especially on the M^1) was G.V. Black (1890:61;

1897:63), who also remarked that it was "always bilateral." This opinion was shared by many dental anatomists, including Diamond (1929:78; 1952:109), Wheeler (1940:219; 1974:238) and Bourdelle (cited by Kraus, 1959). In contrast, Odio de Granda (1927) found that the "tubercle" was bilateral in only "two-thirds" of the individuals in his study group which showed the feature; however, he only considered "negative cusp-outlines" and Carabelli convexities in his investigation.

The most comprehensive recent investigation of lateral asymmetry (on M^1) by a single worker was made by G.R. Scott (1980). His study samples were drawn from North America (Aleut-Eskimo, Southwestern Amerindians), Oceania (Hawaiians, Easter and Solomon Islanders), the Indian subcontinent (Asio-Indians), southern Africa (Bantu, Bushmen), and also included European-derived populations (South African and North American whites). Scott (1980) adopted an eight-class system based on Dahlberg's (1963a) scale and scored his material using Dahlberg's (1956) standard plaque P#12A.

According to this study, the largest proportion of asymmetric individuals in each population were those in which the contralateral molars differed by only a single category of the Carabelli trait-scale, the exceptional samples being the Hawaiians and American whites, where two-rank asymmetry was most commonly found. A high degree of antimeric (M^1) discordance (three or more classes) was rarely observed in any of the groups examined; the frequencies for this type of asymmetry were invariably under 5%. The mean for one-grade asymmetry was 11.2%; for two-grade and multigrade asymmetry, it was 7.2% and 2.2%, respectively.

Most samples had a grade asymmetry (all types) of ca. 20% - 25%. Exceptional groups were the Aleut-Eskimo (9%), the Bushmen (11%), and the Hawaiians (14%). Presence-absence asymmetry was much lower in all populations, ranging from under 2% (Aleut-Eskimo, American whites) to ca. 8% (Bantu), and averaging 5.5% (Scott, 1980).

American aboriginal groups display two different patterns of asymmetry. The Arctic samples, which have the lowest incidence of the Carabelli trait, also have the lowest frequencies of grade asymmetry (9%) and presence-absence asymmetry (1.5%). The Southwestern tribes, which have intermediate incidences of the trait, also have intermediate frequencies of grade asymmetry (21%) and presence-absence asymmetry (6%). There seems to be a correlation between the proportions of asymmetry and trait presence, at least for New World Mongoloid populations (Scott, 1980).

A number of authors have made similar studies of different samples using the same classification scheme and standards. Keiser's (1984b) South African white population displayed frequencies of grade and presence-absence asymmetry (ca. 20% and ca. 2%, respectively) similar to those of Scott's (1980) two white groups. However, Biggerstaff's (1973) data on American (Lexington) whites yielded a much higher figure of 51% (mean for four subgroups for grade asymmetry).

Garn et al. (1966c) and Townsend and Brown (1981) collapsed the eight-class Dahlberg scale into three categories: smooth; concavity; and convexity (although Garn et al. combined the smooth and single-groove forms and eliminated the "high cone" type). The former found perfect rank-concordance for their American (Dayton/Gels) white sample while the latter recorded grade and presence-absence asymmetry proportions of ca. 8% and 6%, respectively, for their Yuendumu Australoid sample. Turner (1967b:8,66) also used a reduced version of Dahlberg's scale, and concluded that Arctic groups (Aleut-Eskimo, Athapascan) manifested less than 5% grade asymmetry.

Other workers have used different classification systems with five categories, and have therefore presented results (for M^1) which are only roughly comparable to Scott's (1980) figures. Baume and Crawford (1980) examined several hybrid (three) and aboriginal (three) groups, which ranged from 16% (Creoles) to 29% (Saltillo Amerindians) in grade asymmetry; these values approximate the mean frequency given by Scott (1980) for several southwestern tribes.

Dietz (1944) and Alvesalo et al. (1975) investigated American (white and black males) and European (Hailuoto Finn) populations, respectively, and found very low proportions of grade asymmetry (ca. 8% - 9%) and presence-absence asymmetry (ca. 0% - 2%). Joshi (1975) recorded an incidence of ca. 11% grade asymmetry for a sample of Gujarati Hindu children.

Simple four-rank classifications have not been commonly used and yield the least precise results. Tsuji (1958) recorded proportions of ca. 9% and 7% for grade and presence-absence asymmetry, respectively, for his pre-adolescent Japanese population; these values approximate figures given for northern Mongoloid peoples (e.g. Aleut-Eskimo) by other workers. In contrast, Meredith and Hixon's (1954) paper on a sample of American (Iowa City) white children presented frequencies of 44% for grade asymmetry and 13% for presence-absence asymmetry (with the smooth and single pit/groove phenotypes lumped together), which are unusually high for any racial group. It should be noted that cases where one antimere had a Carabelli cusp and the other was smooth were very rarely observed in any of the aforementioned studies (e.g. Alvesalo et al., 1975; Scott, 1980; Townsend and Brown, 1981).

Only a few studies have tested the differences in male and female incidences of first molar asymmetry. Scott (1980) found no significant presence-absence dimorphism in any of the five groups examined for sex discordance in asymmetry. Baume and Crawford (1980) stated that sex differences in asymmetry proportions were consistently nonsignificant for all six of their Mexican samples. Biggerstaff's (1973) American white and Townsend and Brown's (1981) Yuendumu Australoid populations also did not show significant sexual differences for antimeric discordance. Overall, there appears to be little evidence for sexual dimorphism in asymmetry frequencies for the Carabelli trait.

The Carabelli trait seems to be autosomal in nature, although there is evidence of low but persistent sexual influence. Among European or European-derived peoples, males almost invariably have a distinctly higher proportion of Carabelli convexities than females, and usually have the higher total trait incidence. Populations of this sort include those from Liverpool, England (Goose and Lee, 1971); eastern Europe (Hanulik et al., 1966); northern Finland (Kirveskari, 1974:37-38); South Africa (Scott, 1980; Kieser, 1984b); Iowa City and Burlington, North America (Meredith and Hixon, 1954; Mayhall et al., 1982).

However, these differences in frequency are not significant (i.e. $x^2 p < 0.05$), on either a grade or presence-absence basis. Exceptions are the Liverpool (Goose and Lee, 1971) and hybrid Skolt Lapp groups (Kirveskari, 1974:37-38). It might be noted that in three of the samples studied, the total male incidence was less than the total female incidence, viz. Chicago whites (Dahlberg, 1963a), Ohio whites (Garn et al., 1966g) and Hailuoto Finns (Alvesalo et al., 1975).

Relatively few studies of non-European Old World peoples have been made. An examination of the South African Griqua (a rather heterogenous group) showed that female dentitions had the higher overall trait frequency (no cusps were recorded), but the difference was not significant (Kieser, 1984a). However, Teso (Uganda) boys displayed a significantly higher incidence ($X^2p < 0.01$) of cusp and "bulge" expressions than Teso girls (Barnes, 1969).

Among Asian populations, Haryana Jat (Kaul and Prakash, 1981) and Hindu Gujarat (Joshi et al., 1972) males displayed significantly higher frequencies than the females. In contrast, males and females of Scott's (1980) Asio-Indian groups exhibited approximately equal proportions of Carabelli convexities and total trait presence. A Japanese sample showed a male predominance in double groove/cusp incidence, although the sexual difference was not significant (Tsuji, 1958). Yuendumu (Australoid) males do show a significantly different pattern (with higher grade-presence frequencies) of trait manifestation, over three classes, than Yuendumu females (Townsend and Brown, 1981). It seems, therefore, that among Old World peoples, males generally show a preponderance of the stronger Carabelli expressions.

The pattern of expression is less clear among the American aborigines. Living Aleut males are likely to display a greater trait incidence than living Aleut females (Moorrees, 1957:38-39), but skeletal Arctic populations (Aleut-Eskimo, Athapascan) show the opposite tendency (Turner, 1967b:66). In both cases, the differences are not statistically important. Pima males exhibit higher frequencies of Carabelli convexities and trait presence, and manifest a significantly different pattern ($X^2p = 0.0001$) of expression, over five classes, than Pima females (Scott et al., 1983; cf. Dahlberg, 1963a). However, in a combined sample of several other Southwest tribes, the females had the larger proportion of trait presence, while the differences were statistically unimportant (Scott, 1980).

In regard to Central and South American populations, males of both the Tarahumara (northwest Mexico) and Lengua (Paraguay) tribes show greater frequencies of Carabelli convexities and trait presence than the females of these groups (Snyder et al., 1969; Kieser and Preston, 1981). In both cases, there are significant sexual differences in trait expression. Overall, American Mongoloids are rather diverse in both degree of sexual dimorphism exhibited for the Carabelli feature and tendency towards male or female trait predominance.

Simple Mendelian (autosomal) models were originally thought to give the most satisfactory explanation for observed Carabelli phenotypes (see Lasker, 1950). Korkhaus (1930) was apparently the first to propose a Mendelian dominant model, based on his European twin studies. Dietz's (1944) examination of American army personnel produced some evidence to support this paradigm, as grade and trait incidences seemed to reflect Mendelian ratios (although the author did not believe this was the best interpretation of his results). Tsuji (1958) stated that a simple dominance model with incomplete penetrance provided the best fit for the data (including pedigrees) recorded for his Japanese population. Hanihara (1963) reached a similar conclusion in his investigation of the Carabelli cusp frequencies found in several "homogeneous" (Japanese, Euro-American, Afro-American) samples and hybrid Japanese-American samples.

Kraus (1951) proposed a codominant, autosomal-allele model on the basis of his analysis of eight Mexican and Papago pedigrees. Turner (1967a; 1967b:68; 1969a) accepted this mode and found no significant differences between observed and expected values in his study of several Arctic groups (viz. Aleut-Eskimo, skeletal and living Koniag, Athapascans). However, his samples were small and the fit with his results imperfect (see also Cadien, 1966).

In opposition to this theory, Kraus (1959) and Goodman (1965) concluded that the codominant paradigm could not account for many of their observations. Also, Sofaer (1970) proved that the methods used by Hanihara (1963) and Turner

(1967a; 1967b:68; 1969a) were invalid. Lastly, Goose and Lee (1971) demonstrated that none of the three possible two-allele models could generate a Hardy-Weinberg distribution of values adequately describing the frequency and pedigree data recorded for their Liverpool population.

Dietz (1944) suggested that a multifactorial model provided the best explanation for observations made on the Carabelli trait. Kraus (1959) came to a similar conclusion, on the basis of his work on Amerindian samples, and a number of other authors have expressed the same belief (e.g. Dahlberg, 1963a; Goodman, 1965; Goose and Lee, 1971). Sofaer (1970) stated that the trait was probably quasi-continuous in nature, an opinion shared by Bailit et al. (1974), Harris (1976), Townsend and Brown (1981), and Scott and Dahlberg (1982). This model, which postulates polygenic inheritance and quasicontinous phenotypic expression, is now the most widely accepted one (Kirveskari, 1974:35; Scott et al., 1983).

6.3.4 Methodology for Carabelli Trait.

Dahlberg's (1963a) eight-grade scale, with Mayhall's (1979b) and Scott's (1980) modifications, was used to score the Carabelli polymorphism (see Figures 16a,16b, pp. 173-174). This was the classification followed by K.E. Wright (1977:19-20). While none of the Zoller Laboratory plaques (P#12A, P#12B, P#14) were available at the University of

Alberta, it was felt that specimen casts approximating Dahlberg's (1963a: Table 1) and Scott's (1980: Figure 1) illustrations would suffice for the purposes of standardization in this thesis.

P.J. Wright (1974:27) adopted a five-rank scheme, based on Kraus' (1959) rating system. This system consisted of the following categories: (1) smooth; (2) one or two pits; (3) one or two grooves; (4) weak tubercle with a fused apex and (5) pronounced tubercle with a free apex. Dahlberg's scale was used in preference to Kraus' scheme because the former was much more comprehensive and precise in its classification of Carabelli variations, and could also be collapsed into fewer categories to facilitate comparisons with other grading standards.

Observations were taken on both sides of each cast, so that side and individual counts could be made. In cases of lateral grade asymmetry (for the individual count), the specimen was assigned to the higher class. All three molars were considered in this study; K.E. Wright (1977:36, 38) also examined all three teeth while P.J. Wright (1974:78-81) only dealt with the first two (M^1 and M^2).

Some problems arose in regard to scoring a few of the Carabelli manifestations. As Kirveskari (1974:37) has noted, the absence of grooves around the "bulge" type of convexity can make it difficult to discern a slight prominence; for procedural purposes, only a distinctive protuberance was accepted for this category. Also, a very careful examination was made of the occlusal and mesiolingual surfaces of the protocone, to ensure that the mesiolingual occlusal groove was not rated as a Carabelli furrow; i.e. that all Carabelli indentations ended distinctly below (cervical to) the mesial marginal ridge. Finally, the shallow, subocclusal, triangular depressions sometimes occurring in the mesiolingual area were recorded as Carabelli variations (see Figure 16a, p. 172).

6.3.5 Observations on Carabelli trait.

The general pattern of Carabelli manifestation was reflected in the upper teeth of the Grimsby sample (see Tables 12a,12b, pp. 202-203). The first molar showed the highest incidence of the trait (68.5%, n=54), with the second and third elements displaying much smaller proportions (7.5%, n = 53 and 5.1%, n = 39, respectively). The first molar also exhibited the only tubercular expressions of the Carabelli feature (5.6%), which took the form of a "broad (positive) cusp-outline" and weak convexities, and the only "negative cusp-outline" phenotypes (3.7%), including both the double groove variation and the Y-shaped furrow (two specimens). Therefore, both trait frequency and intensity decreased posteriorly (from M^1 to M^3) for this Neutral population.

TABLE 12a. CARABELLI TRAIT OF MAXILLARY MOLARS IN THE GRIMSBY SAMPLE: OCCURRENCE BY SIDE.

	FIRST MOLAR		SECOND MOLAR		THIRD MOLAR	
	L SIDE	R SIDE	L SIDE	R SIDE	L SIDE	R SIDE
SEX	#	#	#	#	#	#
MALE						
0	6	8	22	23	9	12
1-2+	12	11	1	1	0	1
3-4++	1	0	0	0	0	0
5-6+++	0	1	0	0	0	0
total	19	20	23	24	9	13
FEMALE						
0	7	8	17	20	13	14
1-2+	9	13	1	2	1	1
3-4++	0	0	0	0	0	0
5-6+++	0	0	0	0	0	0
total	16	21	18	22	14	15
ALL						
0	14	17	42	46	23	28
1-2+	25	28	3	3	1	2
3-4++	3	2	0	0	0	0
5-6+++	2	3	0	0	0	0
total	44	50	45	49	24	30

+ Category includes single ridges, single grooves and single or multiple pits.

++ Category includes negative cusp outlines, i.e. double grooves, Y-grooves.

+++ Category includes strong positive structures, i.e. cusps, cusplike eminences.

TABLE 12b. CARABELLI TRAIT OF MAXILLARY MOLARS IN THE GRIMSBY SAMPLE: OCCURRENCE BY INDIVIDUAL.

SEX	FIRST MOLAR INDIVIDUAL # (%)	SECOND MOLAR INDIVIDUAL # (%)	THIRD MOLAR INDIVIDUAL # (%)
MALE			
0	6 (27.3)	25 (96.2)	16 (94.1)
1-2+	15 (68.2)	1 (3.8)	1 (5.9)
3-4++	0 (0.0)	0 (0.0)	0 (0.0)
5-6+++	1 (4.5)	0 (0.0)	0 (0.0)
total	22 (100)	26 (100)	17 (100)
asym.	9/17 [5]	1/1 [0]	0/1 [0]
FEMALE			
0	10 (43.5)	21 (91.3)	19 (95.0)
1-2+	13 (56.5)	2 (8.7)	1 (5.0)
3-4++	0 (0.0)	0 (0.0)	0 (0.0)
5-6+++	0 (0.0)	0 (0.0)	0 (0.0)
total	23 (100)	23 (100)	20 (100)
asym.	3/14 [0]	0/2 [0]	0/1 [0]
ALL			
0	17 (31.5)	49 (92.5)	37 (94.9)
1-2+	32 (59.3)	4 (7.5)	2 (5.1)
3-4++	2 (3.7)	0 (0.0)	0 (0.0)
5-6+++	3 (5.6)	0 (0.0)	0 (0.0)
total	54 (100)	53 (100)	39 (100)
asym.	12/40 [5]	2/4 [1]	0/2 [0]

+ Category includes single ridges, single grooves and single or multiple pits.

++ Category includes negative cusp outlines, i.e. double grooves, Y-grooves.

+++ Category includes strong positive structures, i.e. cusps, cusplike eminences.

[ ] Number of specimens showing weak expression (1) on one side and absence (0) on the other.

The "broad cusp-outline" grade (see Figure 16b, p. 174) was originally defined by Scott (1973:30-31) as a form intermediate between the Y-shaped furrow and the Carabelli tubercle, but was later placed in the second category (Scott, 1980). It was described as a "large but faint cusp-outline." The Grimsby specimen (Fe9#15, sex unknown) put into this class showed a weak but distinct lingual (M^1) prominence, delimited mesially and distally by two distinct grooves.

While the observations were originally made using a modified version of Dahlberg's eight-rank system, the final statistics were given in a condensed four-division format, after the style of Alvesalo et al. (1975) and Kieser (1984a). The four highest categories of Carabelli manifestation (excluding "high cones," which were not found), were so small in size, totalling just five specimens, that it was more practical to combine them into two larger groups, viz. strong negative expressions (grades 3-4) and strong positive expressions (grades 5-6). The two weakest phenotypes (classes 1-2) often occurred on the first molar (59.3%) and were clearly the predominant Carabelli forms on all upper molars. However, half of all the asymmetric cases on the first molar (6/12) involved a "groove" on one side and a "pit-depression" on the other, suggesting that the two variations are closely related.

There was also a "morphological continuum" between these two negative structures. The characteristic phenotype was that of a short (cingulum?) groove with a triangular (or sometimes circular) indentation at the occlusal end (see Figure 16a, p. 173). In class 1 variations, the groove was the dominant expression, and the "pits" were minute, while in class 2, the triangular depression was the dominant expression, although it was still rather small. In some cases from the latter group, this triangular form lacked a groove on one first molar, but not on the contralateral tooth.

There were just a few exceptions to the general form of the "pit" expression described above. Only one specimen (Fe9#43, LM^2) showed a typical Carabelli pit, as defined previously (see pp. 175-176), on the lingual protoconal face; this was associated with a minute accessory pit (see Figure 16a, p. 173). Dahlberg's (1956) small, subocclusal pit-manifestation was also observed, in several individuals (e.g. Fe7#1, RM^1, Fe9#22, RM^1). Isolated, minute pits were found in two cases (Fe9#42, RM^3; Fe46#1, LM^3), while similar indentations occurred (unilaterally) with grooves, as accessory and adjacent variations on two casts (three teeth).

In regard to positive expressions, the most common kinds were weak, ridgelike elevations. These structures were generally found associated with grooves (as ancillary forms), especially on the first molars, and nearly always occurred as class 1 manifestations. They were recorded as isolated (unilateral) variations in only two cases (on M^1 and M^2), and were not observed on the third molars. As noted above, distinct Carabelli protuberances were rarely seen in the Grimsby sample; there were no examples of the "bulge" phenotype that lacked delimiting furrows.

There was no evidence of strong sexual dimorphism for the Carabelli feature in the study population. The male trait incidence (72.7%) was distinctly higher than the female incidence (56.5%) on the first molar; trait proportions were too low on the other two teeth (M^2 and M^3) for any conclusions to be drawn regarding these elements. The stronger positive expressions were also more commonly found in male dentitions (4.5%) than female dentitions (0.0%). However, these differences in trait and grade (tubercular) frequencies were not significant.

There were 12 casts in the Grimsby sample which displayed some form of asymmetry (on the M^1) for the Carabelli trait. However, as previously noted, half of these cases belonged to the rank 1/rank 2 kind discordance. The other asymmetric specimens were generally of the smooth/single groove type, the only exception being a male individual (Fe9#42), with a negative cusp-outline on one antimere and a weak convexity on the other. Overall presence-absence asymmetry was therefore only 9.3% (5/54), while total grade asymmetry was 30.0% (12/40), using the eight-class system and 15.0% (6/40), using the four-division scale. There was no evidence of strong sexual dimorphism in either presence-absence or grade discordance, although male values were slightly higher.

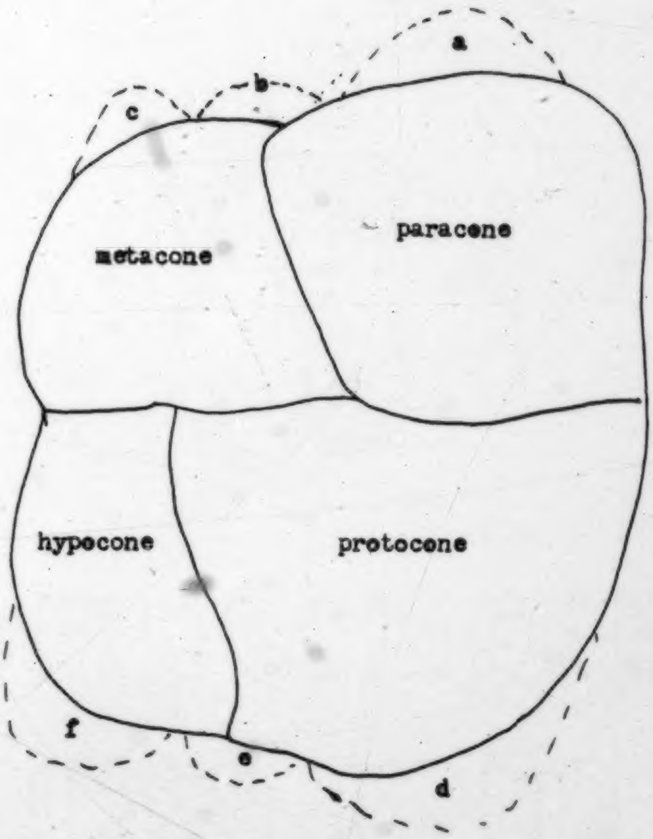
6.4 Lateral cusps on the maxillary molars.

6.4.1 Various aspects of lateral cusps.

Lateral cusps are accessory elements which occur on the "sides" of molar crowns, and only rarely reach the occlusal plane. They consist of two main types: paramolar tubercles, which are found on the buccal surface, and entomolar tubercles, which appear on the lingual aspect (see Figure 17, p. 208). The Cárabelli cusp can be included with the entomolar tubercles; however, unlike these incidental features, it is not an anomaly, but rather a common trait form, and has therefore been considered separately.

Paramolar tubercles were first described by Windle and Humphreys (1887), but the term "tuberculum paramolare" was coined by Bolk (1914; 1916) and used in his seminal papers on these lateral convexities. They may occur at various sites on the paracone, as well as on the metacone or in the notch between these two occlusal cusps. Occasionally, two accessory (usually, mesiobuccal and distobuccal) elements can be observed on the same tooth; in very rare cases, three or even four facial convexities have been found on a single

Figure 17. Lateral cusps on maxillary molars.


a
b
c
metacone
paracone
hypocone
protocone
f
e
d

Various positions (a-f) at which lateral cusps might occur.

molar (Korenhof, 1960:315-326; Kustalogulu, 1962; Woelfel, 1984:225). Paramolar tubercles are generally cone-shaped or cusplike formations; large forms are sometimes associated with a separate or partially-fused radicle (Bolk, 1914; 1916; Pedersen, 1949:134,137).

Entomolar tubercles also occur at several different loci on the upper molars. It should be noted that a large convexity (sometimes, two small protuberances) with a root growth may occasionally be found at the Carabelli site on the third molar (Turner, 1967b:96-97; Taylor, 1978:252-253,275-285). Accessory palatal structures have also been found on the distolingual aspect of the protocone, on the hypocone, and in the notch between these two occlusal cusps. Entomolar tubercles are generally single (sometimes double) cone-shaped or cusplike formations, which rarely manifest a free or partially-fused radicle (Pedersen, 1949:134-137; Kallay, 1966; Taylor, 1978:272,275).

Large entomolar and paramolar structures are composed of enamel and dentine, and may have a pulp chamber, and also a canal when a separate root is present (Kallay, 1958; 1966). These large formations are most likely to occur on the mesiobuccal or distolingual surfaces (rarely, both aspects) of the upper molars, and generally have a free apex (Bolk, 1914; 1916). Slight convexities composed only of enamel are also found; these are associated with weak, single grooves or pits (Kallay, 1958; 1966).

Lateral cusps are generally believed to arise from the basal cingulum (Dahlberg, 1945a; Jørgensen, 1956:72-74; Korenhof, 1960:326-329; Kustaloglu, 1962). However, Kallay (1958; 1966) contends that the large, pulpal paramolar tubercles are formed by the fusion of separate "denticles" with the protocone, a belief evidently derived from Bolk's (1914; 1916) now discredited theory of "dimery" or "concrescence." This hypothesis has been strongly criticized by Korenhof (1960:314-316,326-329), who has used his endocast data to show that paramolar (and presumably entomolar) convexities are clearly related to the buccal (or lingual) cingulum. While most contemporary authors would support Korenhof's view (e.g. Sakai, 1982), Taylor (1978:248,278,335) apparently holds an opinion similar to that expressed by Kallay.

While lateral cusps are best known from human dentitions (among primates), they have also been noted on modern anthropoid teeth. Mediolingual tubercles have been found in the upper molars of baboons and capuchin monkeys (Windle and Humphreys, 1887; Weidenreich, 1937a:76). A small convexity sometimes occurs in a similar position on the second molar of the gorilla, in association with the Carabelli "cone" (Korenhof, 1960:272-273). Paramolar tubercles have been observed in a few baboon, spider monkey and macaque teeth (Windle and Humphreys, 1887; Odio de Granda, 1927; Korehof, 1960:323), and they occur very rarely in chimps and gorilla molars (usually on the M^3). Orangs may occasionally show pits or weak grooves on the buccal cusps of the two anterior molars (Korenhof, 1960:322).

There has been some disagreement over the phylogenetic significance of lateral cusps, which mainly concerns the facial types, although Sakai (1982) found an extra distolingual element on an Eocene tarsioid tooth. Dahlberg (1945a) applied the term "parastyle" (borrowed from palaeontology) to the mesiobuccal tubercles of human upper molars. Kustaloglu (1962) accepted this nomenclature, and also equated the primitive eutherian "metastyle" with the accessory distobuccal convexities sometimes seen in modern man. Paramolar cusps were therefore given some importance as ancestral primate features, as both the parastyle and metastyle occur in the upper dentition of Paleocene and Eocene plesiadapoids, lemuroids and tarsioids (Jørgensen, 1956:120; Korenhof, 1960:318-319; Sakai, 1982).

However, these views have been seriously questioned by other workers. Jørgensen (1956:121,152-154) and Korenhof (1960:329) have demonstrated that mesial paramolar cusps are not homologous with the ancient primate parastyle, because these tubercles are virtually always separated from the typical parastyle locus by a curved or semilunate furrow. Korenhof (1960:329) has also stated that in his endocasts, a distinct vestige of unmodified cingulum occurs between the area of paramolar manifestation and the usual site of the parastyle. Similar arguments can be made in regard to the distal paramolar structures and the metastyle (Jφrgensen, 1956:123-124).

Several authors conclude that lateral cusps lack any phylogenetic significance and are merely fortuitous variations resulting from ontogenetic accidents (Jφrgensen, 1956:72-74; Korenhof, 1960:329; Taylor, 1978:254). Jφrgensen (1956:73) remarked that upper paramolar convexities are not known for any extinct primate forms while Korenhof (1960:318-321) failed to find any maxillary facial tubercles in his examination of fossil prosimian and hominoid teeth, or in his survey of fossil hominid dentitions (Korenhof, 1960:324-325). Robinson (1956:84-85,89-90,96) observed small mesiobuccal protuberances on a few gracile australopithecine molars, but these expressions are apparently true parastyles and not paramolar elements (see Korenhof, 1960:324).

There is some evidence that the mesiobuccal tubercle feature is not an anomaly, but actually a polymorphic character like the Carabelli trait. Kustaloglu (1962) noted the very rare occurrence of a short groove without a protuberance on the paraconal surface, and proposed the existence of an "upper paramolar complex," comprising negative and positive variations. The former would include grooves and probably pits; the latter would consist of weak or small convexities, medium-sized cones or cusps with a "fused" tip, and very large tubercles with a "free" apex (Ibid.; Jørgensen, 1956:153; Korenhof, 1960:316-317; Kallay, 1966). Turner (1985; 1987) has adopted a similar view and outlined a six-rank scale to describe mesial paramolar phenotypes.

Modern human dentitions display a pattern of increasing incidence of paramolar manifestation from the first upper molar to the last one (Korenhof, 1960:326; Kostaloglu, 1962; Turner, 1967b:99,102). Buccal tubercles are so rare on the anterior molar that earlier workers concluded they did not occur on this tooth (e.g. Bolk, 1914; 1916; Odio de Granda, 1927). However, a few authors have reported their presence on this antimere (Windle and Humphreys, 1887; Pedersen, 1949:133,136; Snell, 1959; Kustaloglu, 1962; Kallay, 1966). According to Kustaloglu's (1962) figures, the overall dental proportions for accessory facial cusps (combining all nine study groups) were the following: 0.1% (on the M^1); 2.8% (on the M^2); and 4.7% (on the M^3). Most of these paramolar expressions are paraconal elements; intermediate and metaconal convexities are found much less frequently (Bolk, 1914; 1916; Korenhof, 1960:326; Kustaloglu, 1962).

Kustaloglu (1962) was apparently the first worker to undertake a survey of paramolar cusp incidence among several different groups. Four of his nine populations did not manifest facial tubercles on any of the upper molars (viz. Filipinos, Hawaiians, "Negroes", "Whites". Other non-

Mongoloid samples (Mesopotamians, Melanesians) display frequencies of ca. 2% - 3% on the second molar and 5.5% (for Melanesians) on the third one. American aborigines (ancient Peruvians, Northwest and Southwest American tribes) showed the highest proportions of buccal tubercles on these two teeth: ca. 4% - 5% (on the M^2) and ca. 7% - 12% (on the M^3).

Turner's (1985) study involved a number of American and Eurasian populations of which ten samples scored for the mesial paramolar feature (on M^3) were large enough for purposes of comparison. Arctic Mongoloids displayed the highest frequencies (ca. 6% - 9%) for this character (viz. Aleuts, Eskimos and northeast Asians), while South American natives showed an intermediate incidence (6%) and North American aborigines exhibited the lowest proportions (ca. 3% - 4%) among New World peoples. Southeast Asians ("Sundadonts") and Europeans (Scandinavians) were least likely to manifest mesiobuccal tubercles (1.3% and 1.4%, respectively). It appears, therefore, that Mongoloid (and particularly Eskimoid) groups display the highest frequencies of paramolar cusps, a suggestion made previously by Pedersen (1949:136-137).

The high incidence of upper paramolar cusps found in northern Mongoloid samples has led Turner (1985) to include this feature in his "Sinodont" complex. Mesiobuccal tubercles and other Sinodont traits are thought to have strengthened the cheek teeth of ancestral Amerindian and Eskimoid populations in northeast Asia, by the addition of significant mass to the molar crowns. This would increase the "dental life" of the major grinding elements, under the harsh dietary conditions endured by proto-Mongoloids in the late Pleistocene. However, other workers (e.g. Korenhof, 1960:329) believe that accessory facial convexities lack any sort of functional significance.

Little work has been done on the aspects of asymmetry and genetics in regard to paramolar features. Buccal tubercles are usually unilateral on the first and second molars, but have an approximately equal chance of being bilateral on the last tooth (Odio de granda, 1927; Pedersen, 1949:133-135; Kustaloglu, 1962). Sexual dimorphism is not evident from Pedersen's (1949:134-135) figures. Turner (1967b:98) found no significant difference between male and female paramolar frequencies in his pan-Arctic cranial sample. It seems, therefore, that facial-cusp characters are autosomal in nature and have an increased tendency towards bilaterality on the third molar.

Entomolar features appear to be anomalous variations. They are generally much less common than paramolar cusps and are usually found in the distolingual position. Accessory palatal tubercles occur most often on the posterior molar, probably because this tooth is the one most liable to ontogenetic accidents (Bolk, 1914; 1916; Pedersen, 1949:134, 136). Entomolar convexities are very rarely seen on the first molar, and only a few examples have been noted for the second one (Pedersen, 1949:134; Kallay, 1966). Turner's (1967b:99-102) pan-Arctic samples displayed an incidence of only 0.7% (on the M^3) for mesiolingual tubercles (and 0% on the M^1 and M^2). Pedersen's (1949:134,137) Eskimo skull series showed unusually high dental proportions of 2% (on the M^2) and 4% (on the M^3) for accessory palatal cusps, suggesting that some populations may be more prone to odontological "accidents" than others.

6.4.2 Observations on lateral cusps.

The Grimsby population showed the expected pattern of upper paramolar manifestation, with 1.8% (n = 55) displaying the character on the second molar and 5.1% on the third one. The feature was located on the paracone in all three cases, with the tip always being well below the occlusal surface. In the single male example (Fe36#6003, LM^2), it took the form of a small facial convexity with a broken (fused?) apex. A tiny accessory cuspule with a separate tip was found in one female individual (Fe9#5, LM^3), on the mesiobuccal corner of the last tooth. The sole instance of bilateral expression occurred in another female specimen (Fe17#4, M^3), where the left antimere exhibited a protruding, medium-sized facial tubercle and the right element, a small, fused "cone" at its mesiobuccal corner.

According to the data given above, the paramolar "trait" is much more strongly manifested on the left side than the right.

Distinctive lingual tubercles were not observed in the Grimsby sample. However, a single female individual (Fe46#1) displayed a weak, grooved eminence (associated with several minute pits) on the hypocone of the right posterior molar, and tow tiny pits on the same cusp of the contralateral tooth. These expressions are apparently comparable to distal entomolar convexities.

CHAPTER 7.

MANDIBULAR MOLARS.

7.1 Introduction.

This section will deal mainly with the anatomy, phylogeny, racial variation and genetic aspects of five dental characters: the hypoconulid ("fifth cusp"); entoconulid ("sixth cusp") and metaconulid ("seventh cusp"), the occlusal groove pattern ("Y", "+", "X" types) and the protostylid (mesial paramolar) polymorphism. In addition, the deflecting wrinkle trait, associated with the Y-fissure configuration, will be discussed here. Minor features, viz. supernumerary occlusal and lateral convexities will also be considered in this chapter.

Cusp number, groove configuration and the deflecting wrinkle character will be discussed together in the same subsection. Proportions of the several cusp and groove forms constitute the most widely reported data for the mandibular dentition (Morris, 1970). A number of important studies on American Southwest tribes have considered the frequencies of occurrence of the different fissure patterns and the variable occlusal cones (viz. c_5, c_6, c_7) to be diagnostic of racial affinities, e.g. Nelson (1938), Goldstein (1948), Dahlberg (1951; 1963a), Morris (1965:58-60), Scott (1973:33-38,196-213; Scott and Dahlberg (1982).

Several major papers on Eskimoid groups have also examined these features, e.g. Pedersen (1949:116-117, 129-132), Moorrees (1957:41-46), Turner (1967b:76-86,96-103; 1983).

A few workers believe that the deflecting wrinkle incidence is also of some utility in population comparisons, and have presented statistics on this trait for native American peoples. These include Morris (1970), Scott (1973:35, 200-202), Scott and Dahlberg (1982) and Turner (1983; 1985). Supernumerary occlusal elements will also be dealt with in this subchapter, as a matter of incidental morphological interest.

The protostylid polymorphism and various fortuitous lateral cusps will be discussed in a second segment of this chapter. The former character is commonly considered a "marker trait" for Mongoloid samples when it occurs in high frequencies, and has been examined in several studies of American aboriginal dentitions, e.g. Dahlberg (1951; 1963a), Morris (1965:60), Turner (1967b:87-95; 1983), Scott (1973:36-37,205-208), Scott and Dahlberg (1982). Lateral tubercles include distal paramolar elements (and lingual convexities), but these appear to be anomalous features, and will be dealt with here only as manifestations of minor anatomical concern.

7.2 Occlusal surface features on the mandibular molars.

7.2.1 Anatomical description and phylogeny of occlusal surface features.

Hominid and pongid molars are essentially "quinquetubercular" in structure (see Figure 18a,b, pp. 221-222), consisting of the remnant of the primitive eutherian trigonid, viz. the protoconid and metaconid, and the talonid ("heel") elements, viz. the hypoconid, entoconid, and hypoconulid (Cope, 1886b; Gregory, 1922:362,377; Frisch, 1965:79-80). Only the most primitive early Oligocene catarrhines (e.g. Apidium) show the original mesiolingual cusp (the paraconid). It is not found in fossil or living cercopithecoids, where the molars are bilophodont and basically quadricuspid in form (Gregory, 1922:290,298-299; Simons, 1964). The paraconid was also lost early in hominoid evolution, by the presumed Oligocene ancestors (e.g. Propliopithecus) of the dryopithecines and living apes (Gregory, 1922:286-287,516-517).

The last cusps to be added to the talonid are also the most variable in the human molars. The hypoconulid (c_5) is often greatly reduced or absent (especially in the M_2); it was the final major cone to arise from the protoprimate crown and is the last to appear in the embryonic development of modern man (Gregory, 1922:379,475,513-515; Kraus et al., 1969:110-112,296-304). The entoconid (c_4) precedes the formation of the fifth cusp in both the phylogenetic and

Figure 18a. Occlusal surface features of mandibular molars: dryopithecine pattern. (Adapted from Morris, 1970.)

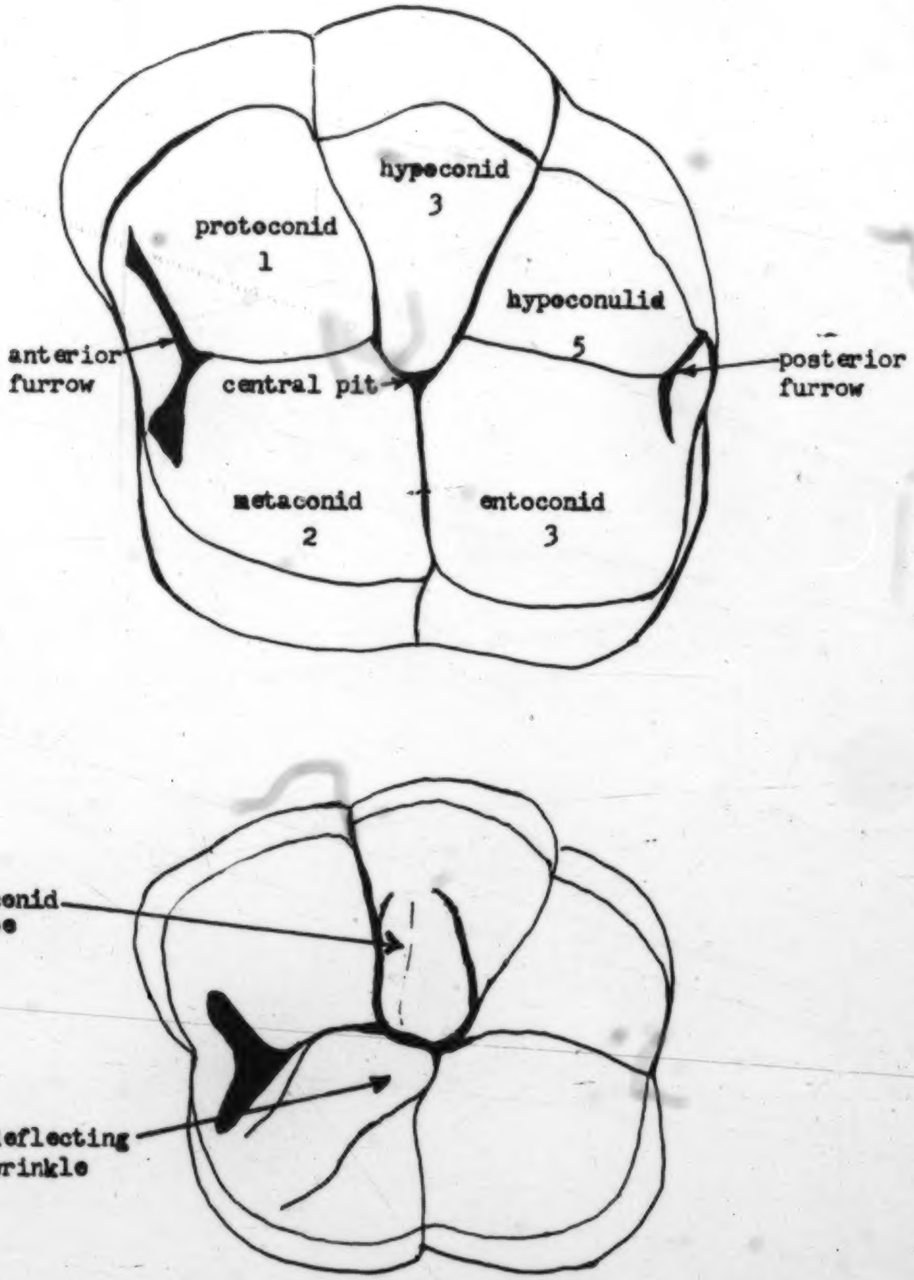
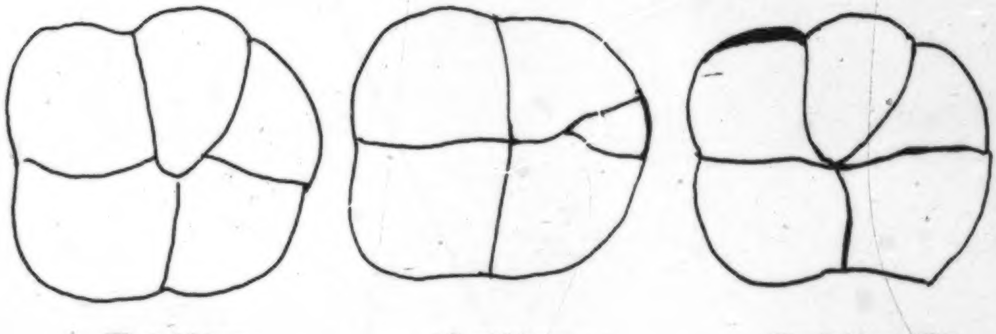

hypoconid
3
protoconid
1
hypoconulid
5
anterior furrow
central pit
posterior furrow
metaconid
2
entoconid
3
hypoconid lobe
deflecting wrinkle

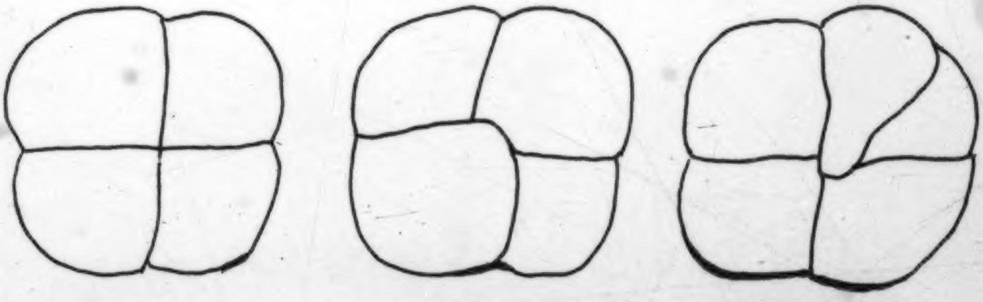
Figure 18b. Occlusal surface features of mandibular molars: cusp and groove patterns. (Adapted from Jorgensen, 1955:197, Figure 1.)



Y5 pattern

+5 pattern

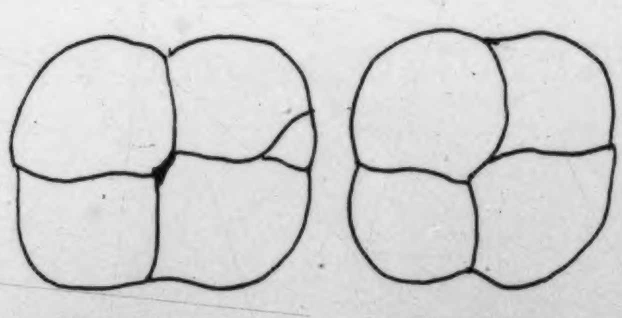
Variation "A"



+4 pattern

Y4 pattern

Variation "B"



X5 pattern

X4 pattern

ontogenetic sequence, and may also be greatly diminished or even lost in contemporary hominid dentitions (Kraus et al., 1969:111,113). However, teeth lacking the fourth cone are so rare that they have only a minor effect on cusp-number statistics (Beynon, 1971; Brabant, 1971).

The basic cusp and groove pattern found on the lower molars were clearly described by Black (1890:77-80,87-89; 1897:79-82,88-89), in the late nineteenth century, but were first given particular designations and phylogenetic significance by Gregory (1916:257,293-294; 1922:328,379) and Hellman (1928). Initially, four types were defined: the "Y5", "+5", "+4" and "Y4" configurations (see Figure 18b, p. 222).

The Y5 conformation predominates on the first molar and the +4 kind on the second, while the last tooth is rather variable in occlusal surface form (Gregory, 1922:504; Hellman, 1928; Kraus et al., 1969:110-111). Jorgensen (1955) introduced the "X5" and "X4" configurations, which are most often seen on the posterior molar and least often on the anterior one; this trend is therefore the opposite of the pattern observed for the Y-groove types. He also noted that the Y-fissure systems found on the two posterior teeth tend to approach the +-fissure form, while a pronounced X-fissure contact was most often manifested on the last element.

The Y-groove conformation was originally described as part of the "dryopithecine pattern", which included a complex of five cusps with mesiodistal and buccolingual fissures, as well as the anterior and posterior fovea (Gregory, 1916:293-294; 1922:328). It has been defined simply as the configuration which results from the contact between the hypoconid (c_3) and the metaconid (c_2) by a number of authors (e.g. Dahlberg, 1945b; Jørgensen, 1955; Turner, 1967b:81; Kirveskari, 1974:43); but strictly speaking, should also include the relative positions of the mesiobuccal and lingual grooves. In the standard Y5 type, the former would clearly be mesial to the latter, on an occlusal surface formed by five "cones" (Gregory, 1934:69; Frisch, 1965:95; Morris, 1970).

The Y5 classification of cusp and groove patterns is complicated by the occurrence of the "deflecting wrinkle" (see Figure 18a, p. 221), especially on the first molar and rarely on the second (Scott et al., 1983). This enamel feature was originally described in fossil hominoids as a bent ridge located on the metaconid, which causes the distal extension of that element (Weidenreich, 1945:71-72,88); it also results in the distal deflection of the lingual groove (Morris, 1970). If the wrinkle is strongly developed, specimens in which the mesiobuccal and lingual grooves are aligned at the lateral edges will still show the hypoconid-metaconid contact. As Morris (1970) has noted, such a configuration represents a "spurious" Y5 pattern, as the fissure would form the "+" type of occlusal surface in the absence of deflecting wrinkle.

The utility of the Y5 classification as a descriptive category has also been reduced by the usage of unorthodox versions. Some authors have simply labelled the wrong set of fissures as representing the Y5 pattern (e.g. Simons, 1964; see also Robinson and Allin, 1966). Others have confused the Y-groove form with +-groove and X-groove configurations (e.g. Anderson, 1969b:94; Bass, 1971:230). In one case, the Y-groove category was even applied to the upper molars (Popham, 1956).

The +-groove type was originally described by Gregory (1916:257; 1922:379) as a cross-like fissure arrangement, but was used by Hellman (1928) as something of a "wastebasket" category, to include all more or less regular occlusal configurations which would not fit into the Y-groove class (see Figure 18b, p. 222). Jørgensen (1955; 1956:65-66) redefined the +-groove pattern as a cruciform variation in which a central, "point-shaped" contact occurs between all four main cusps, so that no two seem to have a wider basal juncture. He also introduced a new fissure type, the "X-groove" class, to label conformations in which the protoconid (c_1) is clearly contiguous with the entoconid (c_4), while the hypoconid and metaconid are clearly separated (cf. Black, 1890:89; 1897:88; Weidenreich, 1937a:93,96).

There are at least two kinds of "transitional" or "borderline" configurations which might be placed in either the +-groove or Y-groove categories (see Figure 18b, p. 222). Jörgensen (1956:65-66) noted the occurrence of an occlusal form ("variation A") in which the mesiobuccal fissure clearly lies anterior to the lingual fissure (as in the Y-groove arrangement), but the basal contact is "point-shaped" (as in the +-groove arrangement), due to strong development of the accessory ridges of the protoconid and entoconid. Weidenrich (1937a:80,88-92) describes several cases ("variation B") where the fissure pattern was of a cruciform type, but the hypoconid and metaconid were connected by a lobe or "narrow wrinkle" extending from the former cusp (cf. Morris, 1970; Kirveskari, 1974:43,45).

Groove patterns are determined by two basic factors: relative cusp size and the mesial shifting of the lingual cusps (Kirveskari, 1974:39). When the metaconid greatly exceeds the protoconid in size, it will tend to have a distinctly greater mesiodistal length, which will create a Y-groove configuration. However, if the protoconid is much larger than the metaconid, a X-groove arrangement will be formed; this will be especially pronounced when the entoconid is also a comparatively large cusp. In cases where the two occlusal elements are about the same size, a

+-groove type will generally result, although this can be altered somewhat by the presence of the deflecting wrinkle or the hypoconid lobe (Weidenreich 1937a:78,80,93).

The same changes in fissure pattern may also be produced by a shifting forward of the metaconid and entoconid, accompanied by the diminution of the former and the expansion of the latter (Frisch, 1965:95,104,110; Skaryd, 1971). This mesial shifting of the metaconid is related to the loss of the paraconid by the proto-anthropoid stock in the mid-Tertiary; the first molar is the most conservative in this regard. While dryopithecine molars generally display only a minor degree of anterior metaconid dislocation, modern chimp and gorilla teeth exhibit a marked degree of displacement, so that the metaconid is often mesial to the protoconid (Frisch, 1965:79-84,140; Skaryd, 1971). Hominid molars also show this tendency to some extent, although the fossil evidence is scarce (Frisch, 1965:85-86).

Two major trends are involved in the transformation of hominoid molars from the primary dryopithecine state to the secondary cruciform condition: the modification of the occlusal surface (as noted above) and the reduction and loss of the hypoconulid (Gregory, 1916:279; 1922:379,475,5[illegible]). According to Hellman (1928), the sequence of stages in this process was - Y5 - Y4 - +5 - +4. However, Dahlberg (1951) proposed that the evolutionary pathway was either - Y5 - Y4

- +4 or (much more frequently) - Y5 - +5 - +4, because it was unlikely that fissure patterns would be more stable than cusp number. In fact, later research proved that the opposite was true; groove configuration was much more "plastic" than fifth-cusp manifestation (Jørgensen, 1955; Moorrees, 1957:42-44; Frisch, 1965:102-103). Erdbrink's (1965; 1967) planimetric studies have demonstrated that the actual order of structural phases was probably - Y5 - +5 - X5 - X4 - +4 - Y4, so that the Y4 would be the most evolved type.

The modern apes and their extinct relatives show the two main trends given above to various degrees. The Y5 pattern is found on the lower molars of early protohominoids, viz. Propliopithecus and Aegyptopithecus, and all dryopithecine genera, e.g. Proconsul, Dryopithecus, Sivapithecus, and Gigantopithecus. However, the +5 configuration has been observed on the posterior tooth of some Limnopithecus species (Frisch, 1965:95-99; Skaryd, 1971).

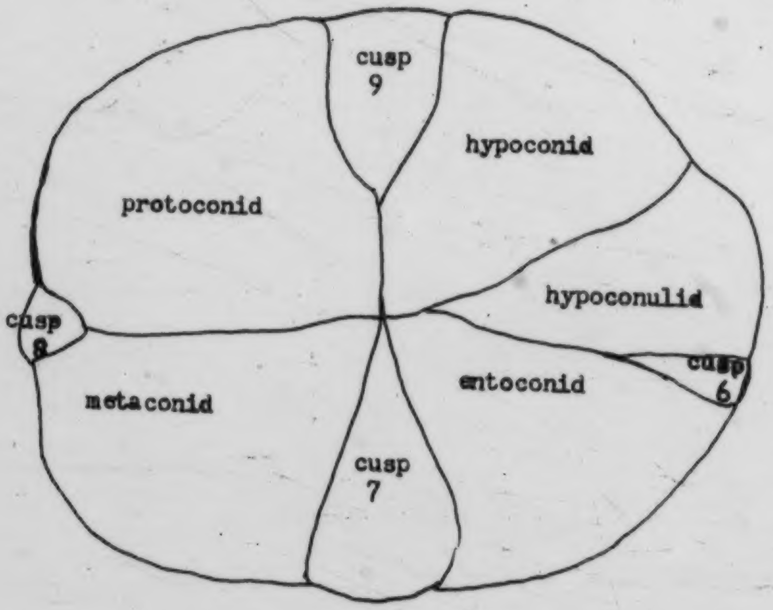
The siamang and orang have the most conservative teeth of living simian forms, with the Y5 arrangement occurring on all three lower molars; gibbon and gorilla dentitions rarely exhibit the +5 occlusal type (under 5%), and only on the last element (Weidenreich, 1937a:85,95; Frisch, 1965:96-98; Skaryd, 1971). Chimp molars display the greatest modification of the primary configuration, especially on the third tooth, where the +5 class constitutes the largest category (ca. 45% - 75%) and the +4 variation the second largest (ca. 20% - 25%). Even the second molar shows notable proportions (ca. 10% - 75%) of the +5 kind of surface (Schuman and Brace, 1954; Skaryd, 1971). The major factor involved in the alteration of the basic hominoid cusp and groove pattern appears to be the reduction (rather than the mesial shifting) of the metaconid relative to the protoconid (Frisch, 1965:84,98-99,104).

Hominids show the same evolutionary trends as pongids, although to a greater degree, viz. the modification of the Y-fissure pattern towards the +- groove configuration (involving mainly the diminution of c_2 relative to c_1) and reduction or loss of the hypoconulid (Gregory, 1916:279; 1922:374,475,504; Weidenreich, 1937a:87-88,94-96; Frisch, 1965:102-104,110-111). Both gracile and robust australopithecines show the Y5 pattern (sometimes Y6, if c_6 present) on the first molar and (with a single exception) on the second molar. However, these teeth are usually transformed towards the +5/+6 configuration, especially in the smaller form, where the first molar characteristically displays the deflecting wrinkle (Robinson, 1956:118, 121; Sperber, 1973:153,166). The last molar, even at this stage, exhibits notable proportions of the +5 type (ca. 20% for Sterkfontein and ca. 15% for Swartkrans specimens) and many of the Y5 arrangements are affected by the deflecting wrinkle (Sperber, 1973:181-182).

The transformation of the cheek-tooth occlusal surface has proceeded further in the fossil hominines. The Choukoutien pithecanthropines generally show a Y5/Y6 pattern with a deflecting wrinkle on the first two molars and the +5 or (occasionally) the X5 configuration on the last tooth (Weidenreich, 1937a:78-79,93; 1945:84,88). The anterior and middle molars of the Mauer jawbone and several Neanderthal dentitions (viz. Ehringsdorf, Gibraltar, Krapina, LeMoustier) display an occlusal form approaching the +5 condition (viz. the "variation B" type), except the Krapina second molars, of which nearly half (ca. 45%) have lost the fifth cusp and exhibit the +4 arrangement (Weidenreich, 1937a:88-92). The Y5 configuration is least modified on the first molar (Bay, 1958; Dahlberg, 1962). The X5 pattern is observed on the posterior tooth of the Mauer and Ternifine (#2) mandibles and in one or two Krapina specimens (Frisch, 1965:100-101). The Y4 type is apparently not found in extinct hominid forms.

The previously mentioned "sixth cusp" or "entoconulid" may be found in recent as well as fossil hominids (see Figure 19, p. 231). is feature is a distolingual accessory element, situated between the entoconid and the hypoconulid, and can (apparently) be derived from either of these convexities or (usually) from the distal marginal ridge

Figure 19. Accessory occlusal elements of mandibular molars. (Adapted from Turner, 1967b:97, Figure 9.)


cusp 9
hypoconid
protoconid
hypoconulid
cusp 8
cusp 6
entoconid
metaconid
cusp 7

between them. The sixth cusp varies in size from a slight ridge ("wrinkle") or nodule to a tubercle distinctly larger than the hypoconulid (Gregory, 1922:378-379; Weidenreich, 1937a:78-79,84-85; Jorgensen, 1956:36-39; Scott and Dahlberg, 1982). The entoconulid may be simply an enamel elevation if weakly expressed, or it may involve a dentine formation if strongly manifested (Turner, 1967b:77).

The sixth cusp occurs occasionally in several dryopithecine genera, e.g. Dryopithecus, Sivapithecus and Gigantopithecus, as well as in the three living pongids (Gregory, 1922:365-366,378-379; Weidenreich, 1937a:84-85; 1945:82,87-88). It is found only in low proportions (ca. 3%) on the posterior tooth of the gorilla. Some chimp samples lack the feature entirely, but others (e.g. a Liberian population) show relatively high frequencies, especially on the first molar (ca. 30%) and the second one (25%), while the lowest incidence (5%) is displayed by the last tooth (Schuman and Brace, 1954; Skaryd, 1971).

The earliest hominids display a sixth-cusp pattern opposite to that seen in the Liberian chimps. The feature is apparently missing from the first molar of the gracile australopithecine (although present on ca. 35% of the M_1's of the robust type), but increases in frequency distalwards in both forms to a level of ca. 50% - 65% on the posterior tooth (Sperber, 1973:152,162,180). The entoconulid is also seen in the dentitions of Oriental pithecanthropines

(Sangiran #5, Mandibles B and D, several Choukoutien specimens) and in some Neanderthal individuals, e.g. Gibraltar, Le Moustier (Weidenreich, 1937a:78,90-91; 1945:42,58,82).

In modern man, the highest incidence and greatest degree of sixth-cusp expression is usually found on the third molar (as in the australopithecines). Hellman (1928) concluded that the frequency of occurrence increased from the anterior molar to the posterior one. However, recent investigators using expanded grading schemes (which considered the weaker manifestations) have demonstrated that the first molars generally display a larger percentage of the feature than the second, with the last tooth showing the highest proportion (Turner, 1967b:77-78,82; Suzuki and Sakai, 1973; Kirveskari, 1974:47-48,88; Saunders and Mayhall, 1982).

The "seventh cusp" or "metaconulid" is another (medio-lingual) accessory occlusal element with phylogenetic significance (see Figure 19, p. 231). It is situated between the metaconid and entoconid, and in man is usually derived from the distal margin of the former, but may also be formed from the mesial border of the latter (Weidenreich, 1945:72-73; Suzuki and Sakai, 1973; Kirveskari, 1974:46). The seventh cusp ranges in size from an enamel nodule or weak ridge ("wrinkle") with a vertical furrow lying mesial and parallel to the lingual groove, to a relatively large wedgeshaped tubercle (with some dentine involvement), which is subequal to the major occlusal convexities (Weidenreich, 1945:72-73; Jorgensen, 1956:40; Turner, 1979; Scott et al., 1983).

The seventh cusp occurs in a number of dryopithecine genera, e.g. Dryopithecus, Sivapithecus and Gigantopithecus (Weidenreich, 1945:82,87-88). It has also been observed in the lesser apes (siamang) and the pongids (orang, gorilla, chimp). Among the latter, the first molar consistently displays the lowest frequencies of the feature; however, the incidence of occurrence increases distalwards in the gorilla (to 35% on M_3), while the second molar shows the highest proportions (10% and 35%) in the chimps and orang (Weidenreich, 1945:82-83).

Extinct hominid species also display the seventh cusp. Among South African australopithecines, both types show the feature on the first molar (ca. 5% - 10%) and it increases in frequency distalwards, to reach the highest level (ca. 15% - 35%) on the posterior tooth (Sperber, 1973:152-153, 166,181). The metaconulid has been observed in the dental elements of Oriental pithecanthropines (Sangiron #5, three Choukoutien specimens), although only in a weak, ridgelike form (Weidenreich, 1945:59,73). It can be seen, as well, in some Neanderthal teeth (Bay, 1958).

In modern man, the highest incidence and greatest degree of metaconulid expression is usually found on the first molar (i.e. the opposite of the australopithecine condition). Recent research has also demonstrated that the second molar is more likely to display a lower frequency of this feature than the last tooth. However, the pattern of manifestation varies in this regard from population to population (Suzuki and Sakai, 1973; Kirveskari, 1974:49,89; Mayhall, 1979b; Saunders and Mayhall, 1982).

The selective advantages conferred by the variable occlusal convexities are not definitely known. Several studies have demonstrated that five-cusped molars are significantly larger (in mesiodistal length) than four-cusped teeth (e.g. Dahlberg, 1961; Garn et al., 1966b,d), so that loss of the fifth element (especially on the M_2) would reduce the surface area available for mastication. Therefore, the recent trend toward hypoconulid reduction and absence would appear to be maladaptive. Turner (1985) has proposed, in regard to Sinodont populations, that the presence of the sixth and seventh tubercles, especially the stronger manifestations, had the effect of increasing tooth-longevity under dentally-harsh conditions by the addition of appreciable mass to the molar crowns.

One groove pattern does not have any obvious functional advantage over another (Turner, 1985). However, Morris (1970) has suggested that the deflecting wrinkle (often associated with Y-fissure systems) serves to plug up the central occlusal pit, thereby increasing the surface enamel exposed to the grinding action of the upper molar elements (viz. the protocone). The hypoconid lobe would also have this effect when strongly developed.

7.2.2 Racial and geographic variation of occlusal surface features.

The cusp-formulae and groove-patterns found in human dentitions have long been examined by dental anthropologists, Hellman (1928) being the first to consider both characters in a systematic way for several different populations. According to his figures, fissure configuration is not as useful for racial discrimination as cusp number, on any of the molars, and later investigations (by other workers) increased the amount of overlap in groove-category incidences between the major geographic stocks (Jørgensen, 1955; Dahlberg, 1963a; Kirveskari, 1974:41). However, it can be concluded that whites commonly display somewhat higher proportions of the +-groove variation than nonwhites, on all three teeth, and that the Y-fissure phenotype is usually found in frequencies of over 60% on the anterior molar and under 20% on the other two elements, for mankind in general (Jørgensen, 1955; Dahlberg, 1963a; Suzuki and Sakai, 1973).

Fifth-cusp manifestation has traditionally been considered a racially-diagnostic character (Hrdlička, 1911; Hellman, 1928; Goldstein, 1931; Dahlberg, 1945b; 1951; 1963a). According to Hellman's (1928) figures, European-derived peoples are most clearly separated from non-Europeans by the distinctly greater absence of the hypoconulid. Four-cusped first molars occurred with a frequency of ca. 10% - 20% in his white samples and ca. 0% - 5% in his non-white populations; in regard to four-cusped second molars, the proportions were ca. 85% - 100% for the former and ca. 50% - 80% for the latter. The last tooth was usually "quadritubercular" in Caucasoid groups (ca. 60% - 65%) and tended to be "quinquetubercular" in non-Caucasoid groups (ca. 50% - 85%).

Recent research has demonstrated that these racial differences are not as substantial as previously thought, and a notable overlap in fifth-cusp incidence may occur. For instance, the Sakhalin Ainu show a 10% figure for four-cusped first molars (Suzuki and Sakai, 1957); while several skeletal European series display a frequency of under 5% for this tooth class, e.g. Medieval Danes, two Megalithic French populations (Jorgensen, 1955; Brabant, 1971). Four-cusped third molars occur in relatively low proportions (ca. 40% - 50%) in a number of Caucasian samples, e.g. Medieval Danes and modern Dutchmen, two Megalithic groups, Medieval and modern Frenchmen (Ibid.).

In regard to "quadritubercular" second molars, there is some intergradation between populations belonging to different geographic stocks. Melanesians exhibit an incidence of almost 90% for this tooth class, while some

Caucasoid groups display proportions of ca. 80% (Dahlberg, 1945b; Erdbrink, 1965). Turner (1985) recorded a figure of ca. 60% for a northwest European sample (scored using an expanded grade-scale), but this result cannot really be compared to data given by other authors. It should be noted that Mongoloid peoples (especially Amerindians) show a great range in quadricuspid frequencies, particularly for the second molar, where intraracial variation is greater than interracial differences with the Caucasoid and Negroid stocks (Turner, 1967b:79-80).

A major question in racial studies has been the degree of comparability of the cusp-number statistics presented by different workers (Goldstein, 1931; Jorgensen, 1955; Kirveskari, 1974:41). The usefulness of cusp-formulae for this purpose was limited by the lack of standard definitions and scoring procedures for hypoconulid expression, and by the presence of occlusal wear, especially on the distal half of the molar (Jørgensen, 1955; Turner, 1967b:77; Morris, 1970). In some cases, this has resulted in anomalously low frequencies for fifth-cusp manifestation: e.g. a first-molar incidence of ca. 50% was given for a Mesopotamian Kish sample (see Dahlbreg, 1963a), while the figures presented by other authors for various populations range from ca. 70% - 100% (Erdbrink, 1965; Suzuki and Sakai, 1973). Turner has recently produced a six-class standard plaque for scoring hypoconulid variation (see Scott et al., 1983); previously, there has been some difficulty in evaluating the size of this element (Davies, 1968a).

Jørgensen (1955) felt that groove configurations were more usable for racial differentiation than fifth-cusp manifestation, because the former are more resistant to wear-obliteration than the latter. However, the identification of different fissure patterns is complicated by the occurrence of the deflecting wrinkle, hypoconulid lobe, and various accessory ridges, and by the fact that some workers classify groove-systems according to the form of basal-cusp contact while others emphasize the relative positions of the mesiobuccal and lingual grooves (Jørgensen, 1956:65-66; Morris, 1970; Kirveskari, 1974:41,45,55). The presence of caries or fillings in the critical area of the tooth is another problem encountered when scoring fissure-type (Kirveskari, 1974:43). Biggerstaff (1968) has even suggested that groove-classes should be abandoned as descriptive categories.

These factors have occasionally led to marked discrepancies among the results given by various authors. Aberrantly-low figures for the Y-fissure class on the first molar have been found for Aleuts (ca. 40%), Mesopotamian Kish (ca. 15%) and American whites (ca. 30%); the general range for this category on the anterior tooth is ca. 65% - 95% (Moorrees, 1957:42-44; Dahlberg, 1963a; Suzki and Sakai, 1973). The most useful application of groove-system (and cusp-formula) statistics seems to be in comparisons of closely-related populations by a single worker (e.g. Goldstein, 1931; Pedersen, 1949:116-117,129-131; Moorrees, 1957:42-46; Turner, 1967b:76-86; Kirveskari, 1974:42-45,87; Scott and Dahlberg, 1982).

Interobserver error is also a factor in statistics reported for sixth and seventh cusp frequencies; especially between the figures given by earlier workers before standard plaques were available and those presented by later authors, in the post-1960 era. The former apparently included only large convexities in their cusp-counts, and either ignored the weaker nodular forms (see Kirveskari, 1974:47) or placed them in a different category (e.g. Pedersen, 1949:116-117,131). In some cases, it was not made clear whether the accessory element observed was the entoconulid or metaconulid (e.g. Kajava, cited by Kirveskari, 1974:47, 49; Kirino and Nakamura, cited by Suzuki and Sakai, 1957). Modern investigators have used the expanded phenotype-scales and plaster plaques of Hanihara (1960) and Turner (1970) for both tubercles. Given these considerations, Mayhall (1979b) has remarked that it is "practically impossible" to make valid comparisons between the older data and more recent information.

A few generalizations about racial variation (on the M_1) can be made on the basis of statistics reported by contemporary dental anthropologists, using the standard scales and/or plaques. Mongolids show high frequencies of the sixth cusp, ranging from ca. 25% - 60%, with two exceptions (Mohave tribe, ca. 10%; Igoolik Eskimo ca. 80%), while Caucasoids display much lower proportions, varying from ca. 5% - 10%. In regard to seventh cusp incidence, recent investigations have demonstrated that there is a substantial overlap between the Mongoloid stock, which ranges from ca. 5% - 35% (except for the central Arctic Eskimo, ca. 80% - 90%) and the Caucasoid stock, which varies from ca. 5% - 25% (Suzuki and Sakai, 1973; Kirveskari, 1974:48-49,88-89; Mayhall, 1979b; Mayhall et al., 1982; Scott et al., 1982; Turner, 1976; 1983; 1985; 1987). These figures are much higher than those given by earlier workers, for closely related populations on the same tooth (see Suzuki and Sakai, 1973).

Deflecting wrinkle frequencies on the anterior molar were first recorded for several different groups by Morris (1970). The highest proportions of this character have been found in the Mongoloid stock: ca. 55% - 80% for Aleut-Eskimo and north Asian samples, ca. 25% - 90% for various Amerindian tribes, and ca. 50% - 55% for Sundadont peoples. The trait incidence for Caucasoid populations ranges from ca. 5% - 35%; South African negros and Bushmen show frequencies of ca. 45% and ca. 80%, respectively, for the wrinkle feature (Morris, 1970; Scott and Dahlberg, 1982; Turner, 1976; 1983; 1985).

7.2.3. Lateral asymmetry and genetic aspects of occlusal features.

The relationship between cusp number (viz. c_5 manifestation) and groove system has only been clearly understood in the last three decades. While both Gregory (1916: 257,279; 1922:379,475) and Hellman (1928) considered these two characters to be more or less separate features, other workers believed that the structural combinations were pleiomorphic attributes; i.e. one allele produced the Y5 surface, another +X5, and a third, Y4/+X4 (e.g. Dahlberg, 1945b). The binary patterns became convenient labels, designating stages of crown modification in the evolution from the primitive dryopithecine state, and were used by early twentieth-century authors to compare the degree of dental "advancement" of the different races (e.g. Nelson, 1938; Pedersen, 1949: 130-131; Dahlberg, 1951).

Jørgensen (1955) demonstrated graphically for a number of racial groups that cusp formula was markedly more conservative than the Y-groove system, especially on the second and third molars, and concluded that hypoconulid-manifestation and occlusal groove-form should be treated as independent polymorphisms. This assertion was supported by Garn et al. (1966a,b) who found no significant correlation between fissure configuration and cusp number on the stable first molar. However, the validity of this result was weakened somewhat by their failure to consider the presence of the deflecting wrinkle and hypoconid lobe and (possibly) by the inclusion of both the Y5 and Y4 variations in the Y-groove category. Most modern authors now classify fifth cusp-presence separately from fissure-type (e.g. Scott and Dahlberg, 1982; Turner, 1983; 1985; 1987).

It should be noted that the emphasis in racial odontology has changed in the last few decades. The earlier workers were concerned with postulating diachronic relationships for the major stocks, in the context of broad evolutionary change. However, contemporary authors stress synchronic estimations of intergroup difference by means of biological distance formulae, which require the consideration of individual traits rather than composite features (e.g. Sofaer et al., 1972b; Berry, 1978; Scott and Dahlberg, 1982; Turner, 1983; 1985; 1987).

The mode of inheritance of the variable cusps (viz. c_5, c_6, c_7) is not definitely established. While the fifth cusp is a primary element, the sixth and seventh tubercles have sometimes been considered developmental "accidents", although Korkhaus (1930) regarded them as heritable characters. Dahlberg (1951) was apparently the first to regard hypoconulid variation as multifactorial in nature. The general opinion among modern workers is that these elements are quasicontinuous features with polygenic modes of inheritance (Dahlberg, 1971; Sofaer et al., 1972a,b; Berry, 1976; 1978; Harris, 1976; Baume and Crawford, 1980; Scott et al., 1983; Turner, 1985).

Kraus et al. (1969:297) remarked that groove pattern probably had a multifactorial basis, and the work of Biggerstaff (1970) and Lee and Goose (1972) seems to rule out simple Mendelian inheritance. Biggerstaff (1968) has even suggested that different fissure configurations are mainly the result of "highly variable" environmental agencies, but it is more likely that these are essentially formed by the genetically-controlled enzymes responsible for final enamel deposition (Kraus et al., 1969:297,302; Dahlberg, 1971). A recent twin study indicated that occlusal groove-type is heritable to a significant degree (Zoubov and Nikityuk, 1978). The current consensus is that the various fissure systems are quasicontinuous characters with a polygenic nature (Dahlberg, 1971; Sofaer et al., 1972a,b; Berry, 1976; 1978; Baume and Crawford, 1980; Scott et al., 1983; Turner, 1985).

The evidence for sexual dimorphism in cusp number is inconclusive. Males more often display the higher frequency for the variable elements on all three molars, according to recent studies on several racial groups, viz. Amerindians, northern Mongoloids, Euro-Americans and East Africans (Suzuki and Sakai, 1956; Turner, 1967a:77-78; Barnes, 1969; Kirveskari, 1974:87-89; Scott et al., 1983). In a few cases, these differences were significant, for the hypoconulid on the first or second molar or both (e.g. living Aleuts, Australian Whites, Mestizo, Tarahumara and

Teso) and for the entoconulid or metaconulid (e.g. Teso, Jomon and Pima) on the anterior tooth (Moorrees, 1957:43-45; Davies, 1968b; Snyder et al., 1969; Barnes, 1969; Turner, 1979; Scott et al., 1983). Turner's (1967b:77-78) skeletal Arctic populations are unusual in that the males show a significantly higher incidence of the sixth cusp on the posterior element.

There are a few cases where overall male predominance in the variable cusps is not clearly manifested (Suzuki and Sakai, 1973; Mayhall, 1979b; Mayhall et al., 1982). In most cases, discrepancies between male and female proportions (for c_5, c_6 and c_7) are not statistically important (Jorgensen, 1955; Suzuki and Sakai, 1956; 1973; Turner, 1967b:77-78,98; 1985; Kirveskari, 1974:43,47-49; Mayhall, 1979b; Saunders and Mayhall, 1982; Scott and Dahlberg, 1982). It can therefore be concluded that the loci responsible for the presence of the fifth, sixth and seventh occlusal elements are probably autosomal in nature.

Sexual dimorphism in groove configuration is either slight or inconsistent for Caucasoid and Mongoloid groups. Differences between male and female frequencies for the different fissure types are not statistically significant in any of the molars for the populations tested (Jørgensen, 1955; Suzuki and Sakai, 1956; Turner, 1967b:83; 1979; 1985; Scott et al., 1983) and are low for populations not tested (Moorrees, 1957:43-44; Snyder et al., 1969; Suzuki and

Sakai, 1973; Kirveskari, 1974:43,87). Comparable data for Negroid samples is largely lacking. The loci responsible for various groove patterns seem to be autosomal in nature.

Lateral asymmetry is usually very low in the first two molars (and relatively high in the last tooth), for both groove pattern and hypoconulid manifestation. Garn et al. (1966a,f) reported a 3% - 4% discordance for cusp number in the first and second molars, while groove-system discordance was 3% in the anterior tooth and 20% in the middle one. Baume and Crawford (1980) found ca. 2% - 8% asymmetry in groove form (Y-type versus +/X-type) in the first molar (except for the San Pablo group, ca. 12%) and ca. 0% - 6% asymmetry in the second tooth. Generally, the Y-fissure configuration is the most stable one, if the fifth cusp is present, especially in the first molar, which shows very low antimeric discordance (0% - 2%). In contrast, the +-fissure configuration is involved in most (ca. 70%) of the discordance displayed by the second tooth, which often exhibits a Y-fissure type on one antimere and a +-fissure type on the other (Dahlberg, 1945b; Garn et al., 1966a,f). Significant sexual differences in lateral groove and cusp asymmetry are uncommon (Baume and Crawford, 1980).

The major accessory elements (c_6 and c_7) show higher presence - absence asymmetry (usually ca. 5% - 15%) than the fifth cusp (Turner, 1967b:80,103; Mayhall, 1979b). However, significant differences between sides in tubercle frequencies have not been found for tested samples (Mayhall et al., 1982). Possible exceptions, involving seventh cusp incidence on the posterior tooth, may be found in two Central Arctic Eskimo groups (both displaying over 20% lateral discordance for M_3). In these populations, the first two molars (M_1 and M_2) exhibit the highest lateral asymmetry for the sixth tubercle and the last two (M_2 and M_3), for the seventh one. Males appear to have somewhat higher proportions of lateral discordance than females (Mayhall, 1979b).

The deflecting wrinkle character has also been examined (mainly in M_1) for sexual dimorphism and lateral asymmetry. The feature is generally bilaterally expressed (Morris, 1970). Significant differences in male and female frequencies are usually not observed (Morris, 1970; Turner, 1979; Scott and Dahlberg, 1982; Scott et al., 1983). It can therefore be concluded that the loci responsible for the wrinkle trait are probably autosomal in nature.

7.2.4 Methodology for occlusal features.

Jϕrgensen's (1955) classification of the different regular groove systems was used in this study (despite the reservations expressed above), in order to bring the procedure employed here into line with that followed by P.J. Wright (1974:41-42) and K.E. Wright (1977:31-32). The Y-fissure type was scored as present if a definite or obvious metaconid-hypoconid (c_2/c_3) contact occurred, while the X-fissure type was counted as present if a definite or obvious protoconid-entoconid (c_1/c_4) contact was found. An occlusal pattern was considered a +-groove form if basal point-contact was observed or the pattern could not be clearly determined to be either of the other two configurations (after Jørgensen, 1955).

A number of extrinsic variables affect the scoring of groove systems. Kirveskari (1974:43-44) remarked that the presence of minute air bubbles in his cast material, at the site of the central occlusal pit, reduced the precision of cusp-contact determination. This was also a problem in the Grimsby samples and in several cases expanded the limit for contact determination, which varied from ca. 0.2 - 0.5 mm. (with the aid of the 10X magnifying glass), i.e. somewhat above Jørgensen's (1955) minimum length for fissure classification (0.2 mm.). Furthermore, in some Grimsby specimens, excess cast material in the critical area obscured the groove arrangement. Caries and attrition have been noted as destructive agencies, in regard to occlusal configuration (Moorrees, 1957:42; Suzuki and Sakai, 1973); the former was a far more important factor than the latter in the Grimsby population. Hypoplastic and restored crowns have caused difficulties in some study groups (see Turner, 1967b:81, 83; Sofaer et al., 1972b; Kirveskari, 1974:43), but these conditions did not occur among the Grimsby people.

The deflecting wrinkle was also examined, because of its relation to the Y-groove pattern, although neither P.J. Wright nor K.E. Wright was concerned with the character. Turner (1979) developed a four-class scale for scoring this trait, but here it was simply marked present or absent, as the scale was not available. A distinct hypoconid lobe or "wrinkle" rarely occurred in the Grimsby sample, so that the feature was not considered further.

The fifth cusp was simply described as being present or absent (see Figure 18b, p. 222). In contrast, P.J. Wright (1974:42) and K.E. Wright (1977:27) rated different manifestations of the hypoconulid. However, as Davies (1968a) and Kirveskari (1974:42,44) have noted, the size of this element is very difficult to estimate, especially without the appropriate plaster standard. Unfortunately, Turner's recently developed six-grade plaque (see Scott et al., 1983) was not available at the University of Alberta.

The hypoconulid was considered to be present when a distinct ridge or nodular elevation (or some stronger variation) occurred in the typical position and was clearly separated by grooves from the other occlusal convexities (following Kirveskari, 1974:42). Neither P.J. Wright (1974:42) nor K.E. Wright (1977:26-27) stated precisely what expression was accepted as the weakest manifestation of the fifth cusp. However, their standard reference (viz. Morris, 1965:60) indicated the existence of the slighter forms of this element.

In regard to the metaconulid and entoconulid, the weakest expressions of Turner's (1970) scales were accepted as present in this study, i.e., secondary ridges associated with minor grooves (see Figure 19, p. 231). K.E. Wright (1977:27-29) considered the same variations (following Kirveskari, 1974:47-48) as tubercular manifestations. P.J. Wright (1974:42-43) did not clearly indicate if the weak ridge-like forms were counted as sixth or seventh cusps, but only scored "present" and "absent" categories. However, the notable proportions given for both elements (Wright, 1974:89,91) imply that these forms were included in his statistics. K.E. Wright (1977:27-29) rated different tubercular phenotypes in a rather subjective fashion, but the accessory cusps were simply classified as present or absent in this study, as neither Hanihara's (1960) nor Turner's (1970) multigrade plaques were available for use.

In addition to the above, other supernumerary occlusal elements (c_8 and c_9) were noted when they occurred, as matters of minor anatomical interest (see Figure 19, p. 231). The numbering of accessory convexities generally followed Turner's (1967b:97, Figure 10) system, except that a newly described (mediobuccal) tubercle was referred to as the "ninth cusp", rather than the distal paramolar elevation (considered in Subsection 7.3.1). This ninth cusp is variable in size, but was simply scored as present or absent.

Individual and side counts were made for all features on each specimen. All lower molars were examined, as was the case in K.E. Wright's (1977:42-45) thesis. P.J. Wright (1974:89-92) considered only the first two teeth (M_1 and M_2).

7.2.5 Observations on occlusal features.

The observations for groove system and cusp formula are presented in combined form (see Tables 13a,b, pp. 252-253), except for the seventh tubercle, which was found only in its weakest expression. While it is recognized that these two characters are separate traits, the traditional crown patterns are a useful way of summarizing morphological information, and continue to be employed by a number of authors for this reason (e.g. Suzuki and Sakai, 1957, 1973; Dahlberg, 1963a; Goaz and Miller, 1966; Brabant, 1971; Sperber, 1973:28,30; Kirveskari, 1974:87; Baume and Crawford, 1978; 1980; Wajeman and Levy, 1979; Hasund and Bang, 1985). Separate statistics are given for the variable occlusal convexities (see Tables 14a,b, pp. 254-255), as there were several cases where cusp number was determinable while fissure arrangement was not. The opposite situation

TABLE 13a. OCCLUSAL SURFACE PATTERNS OF MANDIBULAR MOLARS IN THE GRIMSBY SAMPLE: OCCURRENCE BY SIDE.

	FIRST MOLAR		SECOND MOLAR		THIRD MOLAR	
	L SIDE #	R SIDE #	L SIDE #	R SIDE #	L SIDE #	R SIDE #
MALE						
Y6	3	3	0	0	0	0
Y5	8	9	0	0	0	0
+6,X6	1*	1*	0	1	0	0
X5	0	0	5	5	1	2
+4	0	0	2	1	0	0
X4	0	0	1	3	2	4
Y4	0	0	0	0	0	0
misc.	0	0	0	0	7	6
total	12	13	12	14	12	14
FEMALE						
Y6	2	0	0	0	0	0
Y5	11	9	1	1	0	0
X6	0	0	1	0	0	0
X5	0	0	4	4	1	1
+4	0	0	3	1	0	0
X4	0	0	4	3	6	4
Y4	0	0	1	1	0	0
misc.	0	0	0	0	6	6
total	13	9	15	11	13	11
ALL						
Y6	5	3	0	1	0	0
Y5	24	25	0	0	0	0
+6,X6	1*	1*	1	1	0	0
+5,X5	3	2	10*	10*	2	3
+4	0	0	6	2	0	0
X4	0	0	6	7	8	8
Y4	0	0	1	1	0	0
misc.	0	0	0	0	13	12
total	33	31	32	30	25	25

* Specimen with "+" occlusal pattern present.

TABLE 13b. OCCLUSAL SURFACE PATTERNS OF MANDIBULAR MOLARS IN THE GRIMSBY SAMPLE: OCCURRENCE BY INDIVIDUAL.

	FIRST MOLAR INDIVIDUAL # (%)	SECOND MOLAR INDIVIDUAL # (%)	THIRD MOLAR INDIVIDUAL # (%)
MALE			
Y6	3 (21.4)	0 (0.0)	0 (0.0)
Y5	10 (71.4)	0 (0.0)	0 (0.0)
+6,X6	1 (7.1)*	1 (5.9)	0 (0.0)
X5	0 (0.0)	7 (41.2)	2 (12.5)
+4	0 (0.0)	2 (11.8)	0 (0.0)
X4	0 (0.0)	3 (17.6)	4 (25.0)
Y4	0 (0.0)	0 (0.0)	0 (0.0)
asym.	0 (0.0)	4 (23.5)	2 (12.5)**
misc.	0 (0.0)	0 (0.0)	8 (50.0)
total	14 (100)	17 (100)	16 (100)
FEMALE			
Y6	2 (14.3)	0 (0.0)	0 (0.0)
Y5	12 (85.7)	0 (0.0)	0 (0.0)
X6	0 (0.0)	1 (6.3)	0 (0.0)
X5	0 (0.0)	5 (31.3)	1 (6.7)
+4	0 (0.0)	3 (18.8)	0 (0.0)
X4	0 (0.0)	4 (25.0)	6 (40.0)
Y4	0 (0.0)	1 (6.3)	0 (0.0)
asym.	0 (0.0)	2 (12.5)	0 (0.0)
misc.	0 (0.0)	0 (0.0)	8 (53.3)
total	14 (100)	16 (100)	15 (100)
ALL			
Y6	5 (13.2)*	1 ([illegible]6)*	0 (0.0)
Y5	29 (76.3)*	0 (0.0)*	0 (0.0)
+6,X6	1 (2.6)*	2 (5.1)*	0 (0.0)
+5,X5	3 (7.9)	13 (33.3)*	3 (9.7)
+4	0 (0.0)	6 (15.4)	0 (0.0)
X4	0 (0.0)	8 (20.5)	10 (32.3)
Y4	0 (0.0)	1 (2.6)	0 (0.0)
asym.	0 (0.0)	8 (20.5)**	2 (6.5)**
misc.	0 (0.0)	0 (0.0)	16 (51.6)
total	38 (100)	39 (100)	31 (100)

* Specimen with "+" occlusal pattern present.

** Specimen with "+6/+5" or "x6/x5" cusp asymmetry present.

TABLE 14a. CUSPS FIVE, SIX AND SEVEN OF MANDIBULAR MOLARS IN THE GRIMSBY SAMPLE: OCCURRENCE BY SIDE.

	FIRST MOLAR		SECOND MOLAR		THIRD MOLAR	
SEX	L SIDE #	R SIDE #	L SIDE #	R SIDE #	L SIDE #	R SIDE #
MALE						
6	4	4	1	1	1*	0
5	9	9	7	8	2	3*
4	0	0	5	6	3	5
total	13	13	13	15	6	8
c5	13	13	8	9	3	3*
c6	4	4	1	1	1	0
c7	2	0	11	14	0	0
total	13	11	11	14	13	15
FEMALE						
6	2	0	3	1	0	0
5	14	14	4	4	1	1
4	0	0	10	7	6	4
total	16	14	17	12	7	5
c5	16	14	7	5	1	1
c6	2	0	3	1	0	0
c7	0	0	16	12	0	0
total	11	11	16	12	13	0
ALL						
6	6	4	5*	3	1	0
5	32	34	12	14	3	4*
4	0	0	18	16	9	9
total	38	38	35	33	13	13
c5	38	38	17	17+	4	4*
c6	6	4	5+	3	1*	0
c7	4	2	0	1	0	0
total	32	32	31	31	26	25

+ Specimen with +6/+5 asymmetry present (2.4%, n=42).
* Specimen with X6/X5 asymmetry present (6.7%, n=15).

TABLE 14b. CUSPS FIVE, SIX AND SEVEN OF MANDIBULAR MOLARS IN THE GRIMSBY SAMPLE: OCCURRENCE BY INDIVIDUAL.

SEX	FIRST MOLAR INDIVIDUAL # (%)	SECOND MOLAR INDIVIDUAL # (%)	THIRD MOLAR INDIVIDUAL # (%)
MALE			
6	4 (26.7)	2 (26.7)	1 (12.5)*
5	11 (73.3)	9 (50.0)	2 (25.0)
4	0 (0.0)	7 (38.9)	5 (62.5)
total	15 (100)	18 (100)	8 (100)
c5	15 (100)	11 (61.1)	3 (37.5)
c6	4 (26.7)	2 (11.1)	1 (12.5)*
c7	2 (13.3)	1 (5.9)	0 (0.0)
total	15 (100)	17 (100)	17 (100)
FEMALE			
6	2 (10.0)	3 (16.7)	0 (0.0)
5	8 (90.0)	5 (27.8)	1 (14.3)
4	0 (0.0)	10 (55.6)	6 (85.7)
total	20 (100)	18 (100)	7 (100)
c5	20 (100)	8 (44.4)	1 (14.3)
c6	2 (10.0)	3 (16.7)	0 (0.0)
c7	0 (0.0)	0 (0.0)	0 (0.0)
total	15 (100)	17 (100)	14 (100)
ALL			
6	6 (13.6)	7 (16.7)+	1 (6.7)*
5	38 (86.4)	15 (35.7)	3 (20.0)
4	0 (0.0)	20 (47.6)	11 (73.3)
total	44 (100)	42 (100)	15 (100)
c5	44 (100)	22 (52.4)	4 (26.7)
c6	6 (13.6)	7 (16.7)	1 (6.7)*
c7	4 (10.0)	1 (2.6)	0 (0.0)
total	40 (100)	39 (100)	31 (100)

+ Specimen with +6/+5 asymmetry present (2.4%, n=42).
* Specimen with X6/X5 asymmetry present (6.7%, n=15).

did not occur, except for a few dubious configurations (on M_3).

The first molar invariable manifested the hypoconulid (100%, n = 44) and also showed notable proportions of the entoconulid (13.6%), while the second displayed a much smaller incidence of the former (52.4%, n = 42) and a slightly higher incidence of the latter (16.7%). The last tooth exhibited much lower frequencies of both the fifth and sixth cusps (26.7% and 6.7%, respectively, n = 15). The figures given for the posterior element take into account only the typical crown configurations.

Anomalous third molars showed four to six occlusal convexities, but these were irregularly arranged and varied in size from a small, nodular elevation to an enlarged and bulging protuberance. Aberrant antimeres were often asymmetrical in cusp number, while only one indeterminable individual (Fe9#11, M_2) and a single male case (Fe18#1, M_3) displayed discordance in a standard crown pattern. These showed +6/+5 and X6/X5 combinations, respectively.

The metaconulid displayed the characteristic pattern of manifestation, although only the slightest expression was observed; i.e., a distal ridge and furrow on the metaconid. The trait occurred most often on the first molar (10.0%, n = 40), rarely on the second one (2.6%, n = 39) and was absent on the last tooth (0.0%, n = 31). The seventh cusp was bilateral in the few cases where this was determinable on both sides. It should be noted that there were several specimens (scored as lacking c_7) in which the first molar showed a minor furrow parallel to the lingual groove, but this feature terminated somewhat below the occlusal surface, and there was no evidence of an associated elevation on the distal portion of the metaconid.

Two other tubercles were examined in the Grimsby population. The eighth cusp was found in a few specimens, but sometimes two or three anterior modular elevations were observed instead, and mesial wear prevented the compilation of accurate statistics. The ninth cusp was a much more important feature, and was found in a notable proportion (19.4%, n = 31) of all third molars (on two males and four females). It was bilaterally expressed when determinable on both sides, and varied in size from a small element to a large tubercle, subequal to the major occlusal convexities.

The Grimsby population displayed the usual patterns of groove manifestation. The Y-fissure arrangement predominated on the first molar (89.5%, n = 38), was rarely seen on the second (5.1%, n = 39), and was absent on the third (0.0%, n = 31). The X-fissure system showed the opposite tendency: it was seldom observed on the anterior tooth (7.9%), was much more frequent on the middle one (56.4%), and was found on the posterior element in all individuals (including one asymmetric +4/X4 specimen) with regular occlusal configurations (100%, n = 15). The +-

groove type was the least common kind, and occurred in proportions of 2.6%, 17.9%, and 0.0% (excluding the asymmetric cases) on the three molars (M_1, M_2, and M_3, respectively).

The character of the Y-fissure system observed on five or six-cusped teeth (i.e., c_5 present) differed in some ways from that seen on four-cusped elements. The Y5 and Y6 configurations were invariably bilateral on both the first and second molars, while the Y4 variation was most often asymmetric (2/3 cases on the M_2), there being only one (female) specimen (Fe45#15) in the Grimsby sample with a concordant antimeric expression for this crown type (2.6%, n = 39). Also, the deflecting wrinkle was found (bilaterally) in a minority of individuals (32.4%, n = 34) with Y5 or Y6 arrangements on the first molar, and in the single case displaying the Y6 form on the second tooth. In contrast, four-cusped elements did not show the wrinkle trait. Additionally, it might be noted that in the one (indeterminable) cast (Fe9#46, M_1) exhibiting a strong hypoconid lobe, in a Y5 pattern, the standard basal (c_2/c_3) contact would be maintained, even in the absence of the lobe feature.

Asymmetry in the regular groove configurations was most pronounced in the second molar (17.9%, n = 39). On this tooth, two females showed a +4/Y4 combination; two males and an indeterminable specimen, a +4/X4 pairing, and two other males displayed a +5/X5 association. The first molar did not exhibit antimeric discordance in fissure pattern, while the last tooth in one male individual manifested a +4/X4 condition (6.7%, n = 15).

Anomalous configurations occurred only on the third molar, but more than half the sample (51.6%, n = 31) belonged to this crown class. However, several of these irregular specimens (6/16) showed essentially X4 or X5 patterns, with the addition of the ninth cusp. As noted above, this tubercle was expressed bilaterally. In regard to the other aberrant occlusal forms, including a few similar to the X-fissure type, the two buccal convexities were often uncommonly large, being much greater in size than the lingual elements, especially the entoconid, which was usually rather small. One male individual (Fel5#1) exhibited a six-cusped antimere on one side, with a quasi-X-groove system (of the kind just described), and a X5 arrangement on the other. Combinations of this sort were placed in the irregular crown category, even though one tooth displayed a standard pattern.

The Grimsby population was also examined for possible discrepancies between sides and sexes in trait frequencies. However, lateral differences for the major features were not statistically important. Likewise, there was no evidence for significant dimorphism in male and female proportions.

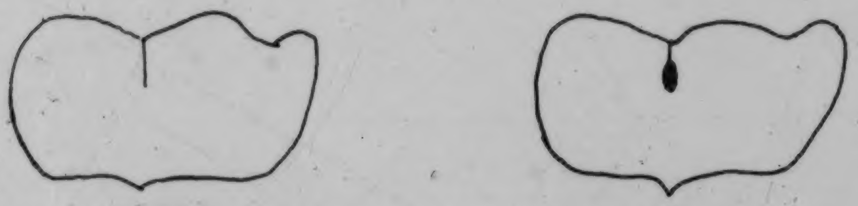
for the various characters (although c_7 was absent in females).

7.3 Protostylid trait and lateral cusps on the mandibular molars.

7.3.1 Various aspects of protostylid trait and lateral cusps.

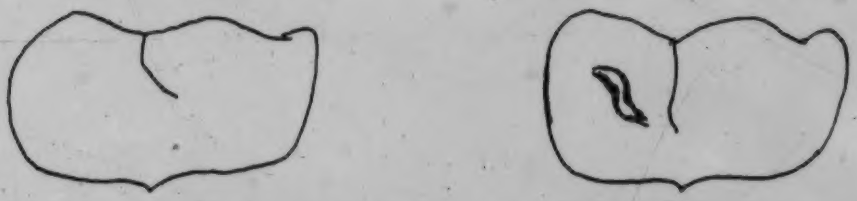
The protostylid polymorphism occurs on the buccal protoconid surface of the lower molars, and includes both negative (groove, pit) and positive cingular variations (see Figures 20a,20b, pp. 261-262). The latter were first intensively studied by Bolk (1914; 1916), who placed them in his "paramolar cusp" category, together with robust but anomalous facial projections. The term "protostylid" was used by Dahlberg (1945a; 1950; 1963a) to refer to specific paramolar structures that occurred bilaterally, had a known phylogenetic history, and exhibited a certain regularity of form. The characteristic manifestation is a prominence running in a mesio-acclusal direction from the cervical end of the protoconid-hypoconid groove, which sometimes lacks a defining "cingular furrow" (Snyder et al., 1969; Mayhall, 1979b). The most pronounced protostylid expression is a large, subocclusal convexity with a free apex; this phenotype appears, very rarely, on the posterior tooth (Kraus et al., 1969:114) and never reaches the maximum size of a Carabelli tubercle (Scott et al., 1983).

Figure 20a. Protostylid trait of mandibular molars: negative expressions.



Grade 0
(trait absence)

Grade 1
(large buccal-groove pit)

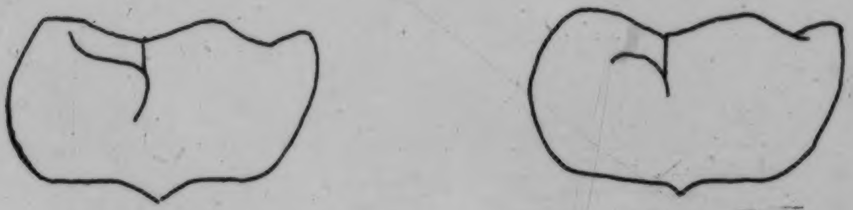


Grade 2
(deflected buccal groove)

Grade 2
(verticle wrinkle)

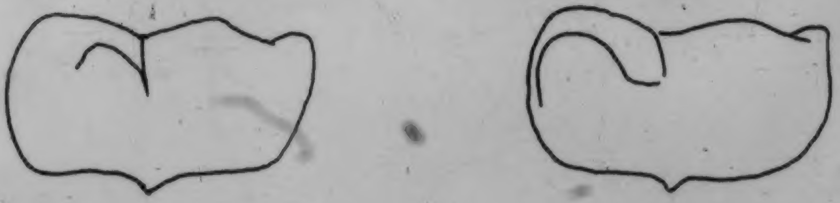
Figure 20b. Protostylid trait of mandibular molars: positive expressions.

(Adapted from Turner, 1967a: 88, Figure 9; Kraus et al., 1969: 114, Figure 1.190.)



Grade 3
(partial cusp, no apex)

Grade 4
(small cusp, free apex)



Grade 5
(moderate cusp)

Grade 6
(large cusp)

Dahlberg (1950; 1951) expanded the known phenotypic range of protostylid variation by including several negative manifestations, in particular, the distal deflection of the protoconid-hypoconid groove and the pit at the end of this groove (see Figure 19, p. 231). The "deflection" occurs in the cervical portion of the groove, and supposedly represents the last vestige of a prominent buccal cingulum on the protoconid (Dahlberg, 1950; 1951; Robinson, 1956:120). Irregularities on the facial surface of this cusp also seem to belong to the protostylid polymorphism; these are usually small indentations or slight vertical furrows (Lasker, 1950; Kirveskari, 1974:53), but the feature may also take the form of a vertical "wrinkle" or ridge (Snyder et al., 1969). The short furrow expression may simply be a remnant of the characteristic lunate or sigmoidal cingular furrow described by Jorgensen (1956:74), which can occur in the absence of a tubercle.

There is some question about the legitimacy of including the buccal-groove deflection and terminal pit in the protostylid polymorphism. Kraus et al. (1969:110-111) treated the indented and tubercular expressions as separate characters. The pit form tends to be relatively common in most populations, is apparently not indicative of any particular racial stock, and shows proportions which are seemingly independent of the other phenotype frequencies (Kirveskari, 1974:52). Also, it is found in a relatively distal position (compared to the other trait variations), and according to some statistical tests occurs independently of the latter (Mayhall, 1979b). The buccal-groove deflection might also be excluded from the protostylid feature, for the same reasons. Some workers have counted only positive manifestations in compiling statistics for this attribute, although the high incidence of facial-groove fillings in their study groups was certainly an important factor in their procedures (e.g., Scott and Dahlberg, 1982; Scott et al., 1983).

It should be noted that the anterior facial-groove pits may vary greatly in size, from minute indentations to elongated depressions to large, deep, oblong or circular concavities (Jorgensen, 1956:69-70; Kraus et al., 1969:110-111). The concavities (foramina caeca) are ca. 1 - 2 mm. in diameter. According to Pedersen (1949:118), these large, deep forms often penetrate to the dentine layer. Foramina caeca are rather common in some Mongoloid groups (e.g., Greenland Eskimos, Apaches, Pueblos) and very rare in Caucasoid samples (Pedersen, 1949:118; Dahlberg, 1950, 1951; Jørgensen, 1956:69-70). Robinson (1956:120) felt that the small pit type and the pronounced invagination were not homologous structures. It is possible that the gene complex responsible for the protostylid trait may also produce (under certain conditions) an enlargement of the terminal indentation.

There has been some confusion regarding protostylid convexities and anomalous cusps which occupy the same position on the second and third molar, but are not found on the more stable first one (see pp. 271-273.) Dahlberg (1945a) initially lumped all of Bolk's lower paramolar formations into the protostylid category; however most of these expressions were robust, projecting tubercles, that never seemed to occur on the anterior molar (Bolk, 1914; 1916). According to Kallay (1966), these stronger manifestations are structures composed of enamel, dentine and pulp layers. In contrast, the much weaker protostylid variations are apparently simple enamel prominences (Dahlberg, 1950; Suzuki and Sakai, 1954; 1957; Kallay, 1966). However, several of the bilateral intermediate types described by Kallay (1966) as enamel and dentine elevations are similar in size and shape to the largest protostylid phenotype.

As noted above, mesial paramolar structures are thought to be derived from the buccal cingulum, an opinion which was first held by some of the older workers (e.g., Weidenreich, 1937a:77,86,93; see Kustaloglu, 1962). In contrast, Bolk (1914; 1916) and Odio de Granda (1927) supported variations of the "concresence" or "denticle-fusion" theory of lateral cusp formation. Kallay (1966) asserted that this theory was correct in regard to the large, projecting convexities, but the weaker protostylid phenotypes were cingular developments. However, Jørgensen (1956:73-74) has described several intermediate stages which seem to bridge the morphological gaps between the two levels of expression and the "typical cingulum". Modern authors accept the contention that the protostylid and other facial tubercles are cingular "specializations" (Dahlberg, 1945a; 1950; Jørgensen, 1956:72-73; Kustaloglu, 1962; Kirveskari, 1974:51; Scott and Dahlberg, 1982; Scott et al., 1983), with the apparent exception of Taylor (1978:248; 277-278), whose "opc" elements are reminiscent of Bolk's paramolar denticles.

The pattern of protostylid manifestation is not of a simple nature. When only the cusp-like variations are counted, the feature is generally the most strongly and frequently expressed on the posterior tooth, and weakest and rarest on the anterior molar (Dahlberg, 1945b; 1963a; Brabant, 1971; Turner, 1979; Mayhall et al., 1982; Saunders and Mayhall, 1982). However, in some groups, the tubercular forms are found most often on the first molar and least often on the last one, e.g. Japanese, Sakhalin Ainu, Pimas (Suzuki and Sakai, 1954; 1957; Dahlberg, 1957). When all phenotypes are considered, the highest incidence occurs on the anterior molar and the lowest on the posterior element in some populations, e.g., Chicago Whites, Skolt Lapps, Japanese Jomon (Dahlberg, 1963a; Kirveskari, 1974:51; Turner, 1979). In other samples, the second or third molar shows the largest proportions, e.g., modern Dutchmen, Arctic dentitions, prehistoric and medieval French and Belgian crania, Burlington whites (Jørgensen, 1956:75; Turner, 1967b:89-90,94-95; Brabant, 1971; Mayhall et al., 1982; Saunders and Mayhall, 1982).

The ancestral pattern of protostylid manifestation appears to be that proposed by Dahlberg (1963a). According to Sperber's (1975:154,167,182) statistics, the gracile australopithecines (Sterkfontein and Makapan fossils) show the highest frequency on the first molar (ca. 90%) and a distinctly lower incidence on the third one (ca. 70%). However, robust (Swartkrans) dentitions display the opposite tendency, with proportions of ca. 30% on the anterior molar and ca. 50% on the posterior element. The strongest variations are found on the first molar in both prehominine types, and range in size from a slight facial bulge to a long (5 - 6 mm.) but narrow prominence; the last tooth exhibits marked asymmetry of expression in the robust form. Deep buccal-groove pits have also been observed in some Swartkrans specimens and small indentations are commonly present (Robinson, 1956:120).

The protostylid feature has also been found in the lower dentitions of fossil hominines. Weidenreich (1937a:77-78,86,93; 1945:84) described the presence of a "bulbous formation" delineated by a sigmoidal furrow (and typically associated with a small buccal-groove pit) on all three molars of the Choukoutien pithecanthropines. Similar but weaker cingular expressions were noted by this author (Ibidem: 41-42; 58-59) in two Javanese jaws: Mandible "D" (RM_1) and Sangiran #5 (RM_2). Striations or "fine denticulations" have been seen as well, on the buccal protoconid surface of the Chinese specimens (Weidenreich, 1937a:77-78,91). These striations and positive cingular expressions likewise occur on the Ehringsdorf and Taubach neanderthal teeth (Ibidem: 91; Bay, 1958).

The value of the protostylid trait as a diagnostic racial feature is not clear. Hanihara (1963, 1966) proposed that high frequencies of the trait were typical of the Mongoloid stock, but some groups of Asian origin apparently lack it entirely, e.g. living Aleuts, Balinese Gilimanuk (Moorrees, 1957:48-49; Jacob, 1967), while others show a very low incidence of ca. 0% - 5%, e.g., Papago and Zuni (Sofaer et al., 1972b). Caucasoid samples rarely display the character, on any of the molars, according to some studies (Brabant, 1971; Mayhall et al., 1982; Saunders and Mayhall, 1982). In contrast, Dahlberg's (1963a) Chicago white population exhibited proportions of ca. 40% - 80% on the three molars, and about half (ca. 45%) the posterior teeth of Jørgensen's (1956:75) modern Dutch series manifested some protostylid form.

It should be noted that in most cases the statistics given by various workers are not strictly comparable. In some instances, different grading schemes were employed (e.g. Jorgensen, 1956:74-75; Brabant, 1971); plaster-plaque standards were not used (e.g., Sofaer et al., 1972b), or only positive cingular expressions were counted (e.g. Scott and Dahlberg, 1982; Scott et al., 1983). Other authors simply excluded protoconid furrows or pits (e.g. Dahlberg, 1963a; Turner, 1967b:87-88; 1979).

Turner (1985) has made the most comprehensive survey of protostylid frequencies in different populations by any single worker, using a nine-grade scale including all known expressions of the feature. He found that proportions of Sinodont groups varied from ca. 15% - 40%, averaging ca. 35%, while Sundadont and Scandinavian samples displayed frequencies of ca. 30% and ca. 20%, respectively. The higher average incidence observed for Sinadont peoples was thought to be related to the dentally harsh conditions under which their Asian ancestors lived in the late Pleistocene, which favoured traits that added mass to the molar crown and increased tooth-longevity.

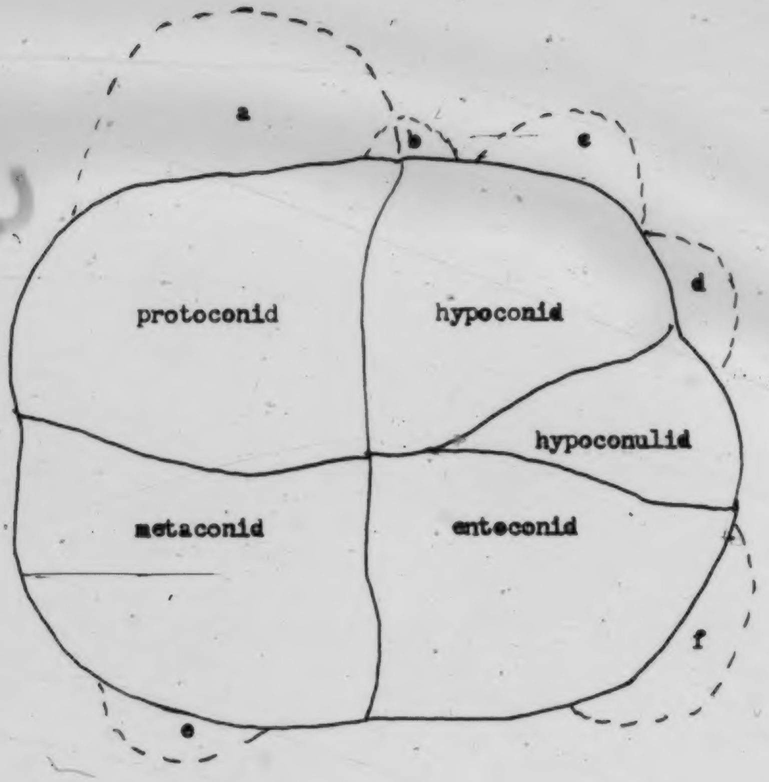
Sexual dimorphism and lateral asymmetry in protostylid expression have also been investigated. Statistically important differences have not been found between opposing sides or antimeres (Snyder et al., 1969; Mayhall et al., 1982). In most studies, discrepancies between male and female trait frequencies are not significant (Snyder et al., 1969; Kirveskari, 1974:54; Turner, 1979; Mayhall et al., 1982; Saunders and Mayhall, 1982; Scott and Dahlberg, 1982). The male incidence tends to be somewhat higher than the female incidence (Turner, 1967b:87-89; Mayhall, 1979b; Mayhall et al., 1982; Scott and Dahlberg, 1982). However, the Pima are exceptional in this regard, as the feature occurs significantly more often on the first molar ($X^2p<0.05$) in males than females (Scott et al., 1983). The difference in proportions approaches a statistically important level for the second molar ($X^2p = 0.07$); this is likewise true for the first molar of Turner's (1967b:87-89) Arctic cranial series ($X^2p = .05 - .08$). On the whole, the protostylid character does not seem to be a sex-linked attribute.

The protostylid feature appears to have a complex, autosomal mode of inheritance. Dahlberg (1950, 1951) was the first to suggest that this was multifactorial in nature. A pedigree study by Dahlberg and Fukuhara (1964) indicated a high degree of trait heritability and supported an autosomal dominant mode of transmission with incomplete penetrance. Turner (1967a,b:89) and Devoto et al. (1972) tested a co-dominant, two-allele model by assuming that the Hardy-Weinberg Law could be applied to their study populations. They demonstrated that the expected results (including observations on the buccal-groove pit) were not significantly different from the actual data (except for the M_3 proportions in Turner's cranial series). However, as

Sofaer (1970) has pointed out, the Hardy-Weinberg Law could not be validly applied in either of these investigations. The protostylid character is now generally believed to be a quasicontinuous attribute with a polygenic basis (Snyder et al., 1969; Dahlberg, 1971; Sofaer et al., 1972b; Kirveskari, 1974:51-52; Berry, 1978; Scott et al., 1983).

As mentioned previously, anomalous convexities also occur on the facial aspect of the lower molars (see Figure 21, p. 272). Robinson (1956:119-120) objected to the assertion that protostylid structures are essentially different from other cingular expressions, found on the mesial protoconid and the hypoconid. However, irregular tubercular features do not occur on the first molar but are restricted to the less stable teeth (M_2 and M_3), are usually unilaterally manifested, and frequently surmount a fused or separate accessory radicle (Bolk, 1914; 1916; Pedersen, 1949:134-135). They may be cusp-like in shape, but often take the form of a robust demicone (sometimes two or more adjacent nodules), merged to some degree with the buccal surface (Bolk, 1914; 1916; Kallay, 1966; Taylor, 1978:307, 309, 313). While these variations are usually found on the protoconid in several positions, e.g. at mesial, mesiobuccal or buccal loci (Ibid.), they may also be observed elsewhere on the facial surface, between the protoconid and hypoconid, on the latter element alone, or between the hypoconid and hypoconulid (Kallay, 1966; Turner, 1967b:96-97).

Figure 21. Lateral cusps on mandibular molars.


a
b
c
d
protoconid
hypoconid
hypoconulid
metaconid
entoconid
f
e

Various positions (a-f) that lateral cusps may occur on mandibular molars; locus a would be the typical Bolk's paramolar tubercle, while locus f would be the distal molar tubercle.

Only a few authors have made statistical studies on the presence of anomalous facial cusps. Turner (1967b:99-100) found only a single unilateral case of a distobuccal tubercle (on the M_3) in his Arctic cranial series (n = 133). Pedersen's (1949:133-135) data given paramolar frequencies of ca. 2% and ca. 6% (on M_2 and M_3, respectively) for his skeletal Eskimo sample (n = 52) and ca. 1% and ca. 3% (on M_2 and M_3, respectively) for his modern Eskimo population (n = 340). The paramolar eminence was generally a small to large mesial (sometimes central) formation, which was usually unilaterally expressed (4/5 on M_2 and 10/12 on M_3). Bolk's (1914; 1916) figures indicate a very low incidence (a fraction of 1%) of mesiofacial convexities for his Dutch specimens. Odio de Granda's (1927) skull collection (representing mostly non-Oriental groups) showed a similarly small proportion of these variations. The divers incidental paramolar types may occur more commonly in Mongoloid peoples than in Europeans (Pedersen, 1949:136-137).

Anomalous cusps also occur (rarely) on the lingual aspect of the second and third lower molars (see Figure 20, p. 262). These are generally manifested on the posterior entoconid face, may surmount a fused or separate supernumerary radicle, and were referred to by Bolk (1914; 1916) as "distomolar" tubercles (cf. Taylor, 1978:312). However, a single (bilateral) case of a small accessory prominence on the palatal metaconid surface was reported by Pedersen (1949:135) for his modern Greenland Eskimo sample (n = 340). entomolar formations are much less commonly observed than paramolar structures. Pedersen (1949:133-137) found distomolar prominences in only a single skull in his cranial series (on M_2 and M_3, n = 52) and a single individual in his modern sample (on M_3, n = 340); these were large, rooted variations, which were more likely to be unilaterally than bilaterally expressed. Entomolar features may possibly occur more often in Mongoloid peoples than in Europeans.

7.3.2 Methodology for protostylid trait and lateral cusps.

Dahlberg's (1956; 1963a) classification of different protostylid variations - as modified by Kirveskari (1974:53) - was accepted in this study for preliminary observational purposes (see Figure 20a,b, pp. 261-262). Unfortunately, neither of Dahlberg's plaster standards (f#13 and f#14) was available for use. K.E. Wright (1977:29-30) followed essentially the same trait scale. P.J. Wright's (1974:43) grading scheme was simpler and less precise, and included the following phenotypes: smooth surface; protoconid furrows and pits; the mesiobuccal prominence (with or without defining grooves) and the tubercle with a free apex. These categories, though, can be made reasonably consistent with the Dahlberg-Kirveskari system by combining classes 5-6, and also 7-8.

However, there was some disagreement between authors regarding the buccal-groove variations. Dahlberg and Kirveskari both incorporated the buccal-groove pit and distal deflection in their protostylid trait complex. P.J. Wright (1974:43-44) considered the former expression to be an independent feature, and did not mention the latter modification, possibly because it was not observed in his small samples due to rarity of occurrence. K.E. Wright (1977:29-30) excluded the terminal pit, but included the groove deflection in her grading scheme. In this study, the mesial foramen caecum was accepted, provisionally, as a protostylid form, and assigned to the first rank of character manifestation. Small or minute pits were not counted because of the difficulty in determining their presence at the end of the anterior facial fissure, a situation which was often aggravated by excess cast material covering the critical area. The deflected-groove phenotype did not present a classification problem, as distinct deviations were not found in the Grimsby population.

A second matter of concern pertains to the class of "surface irregularities". Kirveskari (1974:53) remarked that these expressions were usually small furrows and pits in the protoconid face. P.J. Wright (1974:43) put the furrows and the pits into two separate grades, while K.E. Wright (1977:29-30) added another, rather vague category for slight mesiobuccal deformities. Presumably, that category included the "vertical wrinkle" and "undefined irregularity" mentioned by Snyder et al. (1969). These variations were apparently not observed by P.J. Wright, as no reference is made to them. In this study, protoconid furrows and pits, as well as vertical wrinkles and slight deformities, were lumped together into a single ranked group.

Individual and side counts were made for the protostylid feature on each specimen. All lower molars were examined, as was the case in K.E. Wright's (1977:42-45) thesis. P.J. Wright (1974:89-92) considered only the first two teeth (M_1 and M_2). Also, anomalous buccal and lingual tubercles were noted where they occurred, as matters of minor anatomical interest.

7.3.3 Observations on protostylid trait and lateral cusps.

The observations for the protostylid polymorphism were condensed into a four-category system (see Tables 15a,b, pp. 277-278). As noted above, the large pit phenotype constituted the first grade, while the deflected groove form did not occur, so that the "surficial irregularities" group was assigned to the second rank of presence. The third class represented only the facial prominence which was delineated by a cingular furrow, as the kind lacking the furrow was not found. Robust tubercular expressions were also not observed in the study sample.

TABLE 15a. PROTOSTYLID TRAIT OF MANDIBULAR MOLARS IN THE GRIMSBY SAMPLE: OCCURRENCE BY SIDE.

	FIRST MOLAR		SECOND MOLAR		THIRD MOLAR	
	L SIDE	R SIDE	L SIDE	R SIDE	L SIDE	R SIDE
SEX	#	#	#	#	#	#
MALE						
0	8	4	8	13	4	8
1+	1	2	2	1	0	1
2++	0	0	1	0	3	3
3	1	1	0	0	0	0
1-3	2	3	3	1	3	4
total	10	7	11	14	7	12
FEMALE						
0	14	12	13	9	9	9
1+	0	1	4	3	0	0
2++	0	0	1	0	2	0
3	0	0	0	0	0	0
1-3	0	1	5	3	2	0
total	14	13	18	12	11	9
ALL						
0	29	24	24	24	13	17
1+	2	4	7	5	0	1
2++	1	1	2	1	5	3
3	1	1	0	0	0	0
1-3	4	6	9	6	5	4
total	33	30	33	30	18	21

+ Category only includes large buccal-groove pits.

++ Category includes cingular furrows, small pits and vertical wrinkles.

TABLE 15b. PROTOSTYLID TRAIT OF MANDIBULAR MOLARS IN THE GRIMSBY SAMPLE: OCCURRENCE BY INDIVIDUAL.

SEX	FIRST MOLAR INDIVIDUAL # (%)	SECOND MOLAR INDIVIDUAL # (%)	THIRD MOLAR INDIVIDUAL # (%)
MALE			
0	8 (72.7)	14 (77.8)	8 (61.5)
1+	2 (18.2)	3 (16.7)	1 (7.7)
2++	0 (0.0)	1 (5.6)	4 (30.8)
3	1 (9.1)	0 (0.0)	0 (0.0)
1-3	3 (27.3)	4 (22.2)	5 (38.5)
total	11 (100)	18 (100)	13 (100)
asym.	1/3	1/4	0/4
FEMALE			
0	16 (94.1)	14 (73.7)	10 (83.3)
1+	1 (5.9)	4 (21.1)	0 (0.0)
2++	0 (0.0)	1 (5.3)	2 (16.7)
3	0 (0.0)	0 (0.0)	0 (0.0)
1-3	1 (5.9)	5 (26.3)	2 (16.7)
total	17 (100)	19 (100)	12 (100)
asymm.	1/1	0/5	1/2
ALL			
0	32 (84.2)	30 (73.2)	18 (72.0)
1+	4 (10.5)	8 (19.5)	1 (4.0)
2++	1 (2.6)	3 (7.3)	6 (24.0)
3	1 (2.6)	0 (0.0)	0 (0.0)
1-3	6 (15.8)	11 (26.8)	7 (28.0)
total	38 (100)	31 (100)	25 (100)
asymm.	2/6	2/11	1/7

found. Robust tubercular expressions were also not observed in the study sample.

The Grimsby population did not exhibit the "typical" pattern of protostylid manifestation. The second molar displayed a moderately high incidence of the feature (26.8%, n = 41), mainly because of the relatively large proportion (19.5%) of the foramen caecum phenotype. The last tooth showed the greatest frequency for the trait (28.0%, n = 25), while the first molar presented the lowest figure (15.8%, n = 38). When the large pit category was excluded from consideration, the posterior element again displayed the highest incidence (24.0%), while the two anterior molars both showed much lower proportions (5.2% for M_1 and 7.3% for M_2). However, a strong protostylid expression was only found on the first molar; this was the characteristic mesiobuccal prominence, defined by a cingular groove.

It is notable that the weak surficial expressions (grades 1-2) increased distally in frequency, from 2.6% (on M_1) to 7.3% (on M_2) to 24.0% (on M_3). These were usually tiny pits on the posterior tooth (M_3), while only short furrows and "vertical wrinkles" were found on the two anterior molars (M_1 and M_2). The "wrinkle" type was a slender, curved, ridgelike form (sometimes, two small rugae), occurring on the protoconid face, along with a slight deformity in the area of the buccal groove termination. In two cases, the wrinkle was seen on one side while a partial cingular furrow was observed on the other. The pit and furrow variations could also be manifested together or on opposing antimeres.

There was no consistent evidence for sexual dimorphism in the protostylid feature. While male frequencies on the anterior and posterior molars were two or more times female frequencies, the female incidence for the trait was distinctly greater on the middle tooth. Furthermore, specimens displaying protostylid variations were so few that definite conclusions could not be made regarding the observed sexual differences in attribute proportions.

Gross discrepancies in antimeric trait expression were not found, considering the problem of small sample size. The first molar showed the highest rank discordance (2/6) in regard to protostylid manifestation; this occurred on the presence/absence level for the large pit category. The other two molars exhibited a reasonably small degree of lateral asymmetry (2/11 for M_2 and 1/7 for M_3); the large pit category was involved in one case (on M_2).

Distobuccal tubercles were rarely observed in the Grimsby population; only a single female individual showed (unilaterally) a "cusp-like" variation. This case represented 3.8% - 5.6% of the determinable sample, depending on whether consideration was given to both sides being scorable (n = 18) or at least one side being scorable (n = 26). The specimen (Fe28#52, RM_3) displayed a small, flattened, scale-like eminence, with a free apex, situated at the tooth corner. This apex was well below the occlusal surface, and the eminence was delineated by a weak furrow on the hypoconid face.

Distolingual tubercles were somewhat more commonly observed than facial types, occurring in 6.7% - 10.0% of the determinable Grimsby sample (n = 20, when both sides scorable; n = 30, when at least one side was scorable). Both recorded "cusps" were observed (unilaterally) on the third molars of male specimens. In one case (Fe6#38, RM_3), the accessory structure was a small, weak style-like eminence with a fused apex, on the palatal surface of the entoconid. In the other example (Fe62#69, LM_3), it was a small, scale-like convexity with a free apex that was well below the occlusal surface. This convexity was separated by a strong groove from the distolingual corner of the entoconid.

CHAPTER 8.

COMPARISON OF ONTARIO IROQUOIS POPULATIONS.

8.1 Introduction.

The previous several chapters have dealt with the forms and frequencies of phenotypic variations in the different traits, with attention being focused on the Grimsby sample. However, another major purpose of this investigation was to use the most diagnostic of these dental features in a biological distance analysis of several Iroquoian populations, viz. Grimsby, Shaver Hill, Carton, Kleinburg and Sopher. A related and sequent objective involved the formulation of several general conclusions regarding the utility of odontological characters for such an analysis.

8.2 Tooth-trait categories used for biological distance analysis.

Twenty tooth-trait categories were used in the biological distance analysis of the five Iroquoian skeletal groups. The six traits selected for the upper dentition were: shovelling (on I^1 and I^2); labial ridging (on I^1 and I^2); incisor and canine tuberculation (on I^2 and C^1); hypocone variation (full-sized c_4 on M^1 and M^2); and the Carabelli complex (on M^1 and M^2). Those six selected for the lower dentition were: accessory (one or two) lingual cusp manifestation (on P_4), groove-pattern (+-fissure type on M_1, Y-fissure type on M_2); hypoconulid expression (on M_2); entoconulid and metaconulid occurrence (on M_1 and M_2); and the protostylid polymorphism (on M_1 and M_2). The +-groove and Y-groove forms were selected because their rarity (on M_1 and M_2, respectively) was thought to make them better sample discriminators. Maxillary and mandibular third molars were not used in the analysis, because of the genetic and morphological instability of these elements.

Changes to the sample-sizes and trait proportions given for two of the aforementioned characters (four categories) had to be made for reasons of intersite comparability and rating consistency. Mesiobuccal-groove pits were excluded from the figures for the protostylid feature (on M_1 and M_2), as data for the large, deep form was not available from the statistics given by P.J. Wright and K.E. Wright, and pit types may not belong to the trait complex. Also, five-cusped maxillary molars were subtracted from the samples considered for hypocone expression (on M^1 and M^2), as the additional large convexity (distal tubercle) markedly affected the size of the fourth element and apparently did not occur to any prominent degree in the four ossuary populations.

The dental characters used for the statistical comparison of the five Iroquoian samples showed a reasonably low intra-observer error in repeated scoring trials (generally, 5% - 10%). The two features causing greatest difficulty were (1) shovelling (viz. strong versus moderate classes on I^1 and I^2) and (2) hypocone manifestation (viz. 4 versus 4- categories on M^1 and M^2); these varied in a rather gradual and continuous manner from a state of pronounced expression to one of absence. The second attempt at ranking each of these traits, using an enlarged series of "standard" casts for phenotype-comparison, resulted in a discrepancy of some 15% - 20% (for both cases) between the two evaluations. A third rating exercise was undertaken, specifically for the shovel-shape and hypocone attributes, again using the enlarged cast series, and this procedure reduced the intersessional grading inaccuracy to ca. 5% - 10%.

Problems in ranking shovel-shape form and hypocone size have also been mentioned by Scott et al. (1983) and Greene (1967:11-12), respectively. It should be noted that K.E. Wright's (1977:11) "overall repeatability" in scoring was ca. 85%, although she unfortunately failed to determine her rating consistency for the individual traits. P.J. Wright did not conduct multiple grading sessions, but because his experience in dental morphology was at least equal to K.E. Wright's, it can be assumed that his intra-observer error for the same features would have about the same magnitude.

The selected traits had to have genetic qualities suitable for biological-distance analysis. All these features were of a stable nature, having a traceable phylogenetic history, which in some cases (e.g. the

Carabelli cusp) was of great duration, as well as an apparently high degree of heritability, as determined by twin and affine-resemblance studies. First incisor and first molar characters display a higher degree of heritability than second incisor and second molar characters; however, the differences in values are not significant (Sofaer et al., 1972a).

None of these dental features showed consistent sexual dimorphism, with the exception of shovelling on the central incisor (I^1), and this was only true when a very large, combined sample (ca. 10,000 - 20,000 individuals) was under consideration (see Harris, 1980). It should be noted that the skeletal material from the four ossuary sites could not be sexed and consequently, trait frequencies could not be weighted to compensate for male-female differences. Therefore, the selected attributes had to have an autosomal mode of transmission.

A potential problem affecting the use of dental features in a biological distance formula is the possibility of intertooth trait correlation, which implies that the same genetic complex controls a specific character (or characters) on several different elements. If more than one of these elements is included in the formula, there will be a certain redundancy (and therefore, an imbalance) in the information utilized to discriminate between populations. This concept of a "sphere of influence" or "developmental field" governing several attributes found on adjacent teeth of the same class was introduced by Butler (1939).

Dahlberg (1945b; 1951) applied the concept of "developmental fields" to the human dentition to account for gradients of expression found in different tooth districts. He suggested that the four dental classes - incisors, canines, premolars and molars - were each governed by separate morphogenetic "spheres of influence", with the maxillary spheres possibly being distinct from the mandibular ones. The features controlled by each sphere would be most strongly manifested on the phylogenetically stable "key tooth" at one pole, and weakest at the other extremity of the field; e.g. the Carabelli cusp was most frequently and intensely expressed on the first upper molar, and was rarest and smallest on the last one.

However, as noted above in the relevant parts of this thesis, the morphogenetic spheres are rather unstable for nearly all the traits considered here. Some populations displayed a frequency gradient (e.g. on M1, M2, M3) for some dental characters (e.g. the protostylid) exactly opposite to that expected on the basis of the field theory, while many exhibited the lowest proportions of a feature on an intermediate tooth (e.g. on M2). Only the very ancient Carabelli complex consistently showed agreement with field predictions among the numerous different racial or geographic groups examined, although even in this case, there were still a couple of apparent exceptions. The limited data available for australopithecine teeth suggests that Dahlberg's developmental fields were much stronger in the older hominids than in recent man, who seems to manifest greater dental variation, perhaps due to the reduction of selective pressures.

Several statistical investigations have been made to determine the degree of trait association that exists between different teeth supposedly belonging to the same field. A number of studies have demonstrated a highly significant correlation between the shovel-shape expression on the first maxillary incisor, and that on the second (e.g. Carbonell, 1963; Suzuki and Sakai, 1966; Sofaer et al., 1972a; Scott, 1973:66-69; Berry, 1976). A consistent relationship between shovelling and labial ridging (on both I^1 and I^2) has been found for some racial groups (Suzuki and Sakai, 1966; Kieser and Preston, 1981) but not for others (Moorrees, 1957:26; Kieser, 1984a). It should also be noted that the shovelling character may be controlled by the same genetic complex in both upper and lower jaws (Suzuki and Sakai, 1966; Scott, 1973:66-69; 1975).

Some studies have suggested that the degree of shovelling on the upper incisors could be related to the development of lingual cusps on these two elements. Suzuki and Sakai (1966) demonstrated this to be true for their propositi, but only for prominent first incisor convexities.

Berry (1976) found a significant interdependence between shovelling on the central incisor and "cingular nodules" on the lateral tooth, and a few of Scott's populations showed a similar correlation (between I^1 shovelling and I^1 tuberculation). However, Moorrees' (1957:26) and Carbonell's (1963) samples did not display any consistent linkage between these two features (on the I^2) and neither did most of Scott's (1973:67,69-72) native groups, on the central incisor. None of the latter exhibited a statistically important connection between shovelling (on either I^1 or I^2) and the tuberculum dentale on the second incisor; however the tubercle character on that tooth was significantly associated, more often than not, with the same attribute on the first incisor.

Several investigations have indicated that the upper canine probably belongs to the incisor field, and others, that it may be affected, as well, by the premolar sphere of influence (e.g. Turner, 1969b; Berry, 1976). One study supporting the former proposition found that shovelling on the maxillary incisors was strongly correlated with lingual and labial marginal ridging, and with the basal tubercle on the maxillary canine (Suzuki and Sakai, 1966). In Scott's (1973:67,69-72) aboriginal populations, shovelling on the upper central (but not the upper lateral) incisor was also found, in a few cases, to be significantly associated with the lingual cusp of the upper canine. However, in the majority of Scott's samples, the two features (on I^1 and C^1) were expressed independently of each other. Additionally, the "cingular nodule" character occurring on the first incisor has been shown to be statistically linked - in most of Scott's (1977b) groups - to that manifested on the canine, but the same relation does not generally occur between the second tooth and the canine (cf. Berry, 1976).

In regard to the anterior cheek dentition, Berry's (1976) investigation demonstrated the occurrence of a statistically important correlation, for some populations, between lingual occlusal tubercles and occlusal pits on the lower second premolar. Palatal cusp number in the first premolar (P_3) was significantly associated with that in the second (P_4) in most of Scott's (1973:67,77-78) study groups. However, of the aforementioned traits, only the last named (accessory lingual cusps on the P_4) was used in the intersite sample analysis.

The most important upper molar features used as population-discriminators are hypocone variation and the Carabelli complex. Hypocone expression in the first molar was highly correlated (for all groups considered) with that in the second, according to one study (Scott, 1973:67,72-74), and cusp number in the second tooth to that in the last, according to another (Sofaer et al., 1972a). However, Greene (1967:24-25,35) demonstrated for his cranial series that hypocone reduction in the anterior molar was independent of that in the middle one. Carabelli manifestation on the former element (M^1) was shown to be statistically linked to that on the latter (M^2) in most of the samples tested by Scott (1973:67,72-74).

Both Keene (1965; 1968) and Scott (1973:67,72-74; 1979) found that a strong association occurred in their populations between hypocone development and the Carabelli polymorphism (on M^1 and M^2, especially the former). However, other investigations have indicated that these two dental characters are autonomous attributes (Greene, 1967:25,35; Sofaer et al., 1972a; Berry, 1976). It might be noted, though, that Berry (1976) has demonstrated that the metaconule trait (in its larger forms) and the Carabelli cusp are interdependent on the anterior molar in one of her two tested samples.

The traits of interest on the lower molars are groove system, hypoconulid-manifestation, accessory occlusal elements (c_6 and c_7) and the protostylid complex. According to several investigations (e.g. Jorgensen, 1955; Garn, 1966; Garn et al., 1966a,b; Greene, 1967:25-27,35; Berry, 1976), fissure pattern (on M_1 and M_2) is independent of cusp number (i.e., c_5 presence); Sofaer et al.'s (1972a) study is exceptional in this regard. The latter also found a high correlation for groove configuration on the anterior and middle molars, and cusp number on these two elements, but most research has indicated that both features are autonomously expressed on each of these teeth (Greene, 1967:27-29,35; Berry, 1976).

The seventh cusp showed a significant association on the first and second lower molars in a few tested samples as did the sixth cusp, although in the case of the latter, most groups did not manifest such a relationship (Scott, 1973:67, 77-79). This tubercle (c_6) has been statistically linked to the hypoconulid (c_5) by one worker (Turner, 1967b:76-78), but not by other authors (Scott and Dahlberg, 1982; Scott et al., 1983). Also, Goaz and Miller (1966) demonstrated a very strong negative correlation between the Y5 pattern and the protostylid complex on the anterior molar; this result, however, has not been duplicated in other investigations (e.g. Scott and Dahlberg, 1982; Scott et al., 1983).

There has been a certain degree of ambiguity regarding the independence of the upper and lower molar fields. Dahlberg (1951, Figure 4) implied that the two jaws were controlled by autonomous "spheres of influence", while Butler (1961) has suggested that some traits at least are determined in both dentaries by a single genetic complex. Evidence can be provided to support either position. A number of studies have found a high correlation between the Carabelli polymorphism (on M^1) and the protostylid character (on M_1), in several different samples (Suzuki and Sakai, 1954; Scott, 1973:67,75-76; 1975; 1978). Barnes (1969) found a significant association between the Carabelli tubercle and the seventh cusp in his study group. Also, Sofaer et al. (1972a) found that the hypocone and hypoconulid features were statistically linked on the upper and lower molars (M^2 and M_2), and so were hypocone expression and fissure configuration (M^2 and M^3 with M_1 and M_2).

In contrast, several investigations have indicated a genetic autonomy for maxillary and mandibular dental characters. The Carabelli trait (on M^1 and M^2) has been shown to be independent of both fifth-cusp expression and groove pattern (on M_1 and M_2) by a number of workers (Garn et al., 1966c; Sofaer et al., 1972a; Berry, 1976). Greene (1967:29-32,35) and Berry (1976) found that for their skeletal and living populations, hypocone development was statistically unrelated (for all tested molar samples) to cusp number (i.e. c_5 presence) and fissure system. Furthermore, Goaz and Miller (1966) demonstrated that the Carabelli polymorphism (on M^1) and the protostylid feature (on M_1) were not significantly correlated in their study group.

The dental attributes which were used in the biological distance formula and were examined in this section generally showed only a slight or inconsistent association with each other. The two exceptions to this conclusion were shovelling on the two upper incisors (I^1 and I^2) and the Carabelli complex on the first two upper molars (M^1 and M^2). The maxillary shovelling trait especially manifested a strong correlation between the central and lateral elements in several extensive investigations. However, as Moorrees (1957:28) has noted, the narrower form of the second incisor may often cause an error in assessing the degree of shovelling (on I^2 relative to I^1), and Scott et al. (1983) have produced a separate scale for rating the character on this tooth, essentially treating it as a separate feature.

The Carabelli phenotypes manifested on the first two upper molars have been found to be highly correlated in two studies (Sofaer et al., 1972a; Scott, 1973:67,72-74). It should be noted, though, that in Scott's more extensive investigation (which tested five rather than two samples), the groups examined showed as consistent an association between the Carabelli polymorphism and the protostylid complex (on M^1 and M_1) as between Carabelli trait expression on the first molar and that on the second one. It seems rather odd that the (genetic?) linkage between two apparently separate features in two different jaws should be just as strong as that between a specific character on one tooth and the same character on an adjacent element. The real significance of such statistical relationships is a matter of some dispute (see Molto, 1983:171-173).

A number of possible epigenetic linkages have been indicated for traits located in different fields. Labial shape (of I^1) and the shovel-form and cingular nodule (on I^2) have all been shown to be correlated with Carabelli trait development on the first molar, in some populations (Dietz, 1944; Sofaer et al., 1972a; Berry, 1976). Cingular nodules (on I^1 and I^2) have also been statistically connected to accessory buccal cusps on the lower and upper second premolars, respectively (Berry, 1976). Some interdependency has been demonstrated for shovelling (on I^2) and the hypoconulid (Sofaer et al., 1972a). Lastly, the canine (C^1) tubercle has been found to be significantly associated with hypocone expression in a minority of samples tested by Scott (1973:67,74-76), on the anterior maxillary molar, and in most of his groups on the middle tooth. These relationships are not well understood and are probably of dubious value; modern workers tend to ignore them (e.g. Scott and Dahlberg, 1982).

Opinions vary in regard to dealing with the problem of correlated dental or skeletal characters. Sofaer et al. (1972b) remarked that trait autonomy was of minor importance when only relative differences between groups were being considered. Sjøvold (1977) recommended treating recognized attributes as independent, even if some were statistically linked, because the overall pattern of association was generally rather low, so that "serious distortion" would not occur in the resulting distance value. This approach increases the number of features that can be used in the analysis, and therefore has the advantage of reducing the effect of random factors (e.g. genetic drift) on the final calculation. However, some workers have adopted other procedures for handling the difficulty posed by pleiogenic complexes (see Molto, 1983:171-173).

Finally, it should be emphasised that virtually all the studies cited above have used the wrong statistic to determine trait autonomy, viz. the X^2 function (e.g. Berry, 1976), or a modified version of this parameter which accounts for sample-size disparities (e.g. Scott, 1973:64-66). As Molto (1983:134-136) has noted, the X^2 technique actually estimates the homogeneity of incidence in two different samples (sides, sexes, etc.); the phi-coefficient is the correct formula for testing the independence of occurrence of a feature, ~~on~~ a lateral or serial basis (i.e. on different antimeres or different teeth). Molto found that none of his 24 discontinuous cranial characters were correlated according to the phi-coefficient trials, but 21 were significantly associated according to the X^2 analysis. The X^2 measure is therefore likely to give an exaggerated impression of the real degree of linkage between various attributes, and also to make several spurious statistical connections.

8.3 Consideration of biological distance formulae.

The distance statistic chosen here was the Grewal-Smith (1962) Mean Measure of Divergence (MMD), which is presently considered the best formula for comparisons using qualitative morphological data (Sjovold, 1977; Molto, 1983:14,180), such as quasicontinuous dental characters (Scott and Dahlberg, 1982). The MMD does not provide the graphic depictions (of phenetic relationships) available for more than three samples with the Harpending-Jenkins' Coefficient of Kinship (Scott et al., 1983). However, it does not require that genetic drift be the agent primarily responsible for intergroup variance, a dubious assumption according to several authors, who have emphasized the effect of selective factors on human dentitions (Dahlberg, 1951; 1963a,b; Beynon, 1971; Turner, 1983; 1985). The MMD also does not assume that the proportions of complex dental traits can be substituted for the frequencies of simple Mendelian genes, which the Coefficient of Kinship was originally designed to handle.

The MMD statistic offers several advantages over other distance formulae used in the past. For instance, it corrects for large disparities in group size, unlike Pearson's Coefficient of Racial Likeness and Sanghvi's G test (Rao, 1955; Scott and Dahlberg, 1982). Also, it accurately reflects (in terms of percentage variance) the differences between samples with low trait proportions, relative to those between samples with high proportions, unlike Sanghvi's G test (formerly, Sanghvi's X^2), which exaggerates the former compared to the latter. Furthermore, it is possible to determine the significance of the MMD values calculated for several populations, as well as the magnitude of the dissimilarity between each (Sjøvold, 1973), which cannot be done for the X^2 or Sanghvi's G techniques (P.J. Wright, 1974:221; K.E. Wright, 1977:63).

The MMD has been the preferred statistic in several dental studies; e.g. Berry (1976), Scott and Dahlberg (1982), Sofaer et al. (1986). In each case, there has been good general agreement in regard to intergroup affinities with estimates based on gene frequency data. It should also be mentioned that K.E. Wright (1977:51-53,60-66) applied the MMD to her analysis of four ossuary samples, and found it more useful, overall, than the Sanghvi's G test.

There are five conditions necessary for the use of dental characters in the MMD equation, for the purposes of interpopulation analysis (Berry, 1976). These are

(1) trait manifestation is largely genetically controlled;
(2) trait occurrence is not influenced by sexual dimorphism;
(3) trait occurrence is not influenced by age-related factors;
(4) traits are independently expressed; and
(5) no one trait disproportionately influences the final calculation.

The review of the features employed in the MMD statistic indicates that the first four requirements are likely to apply in this study, except for age-related factors (e.g. wear) which were not specifically discussed. However, there is no evidence to indicate that these factors played a significant role in biasing the scorable sample.

In regard to the last condition, Scott (1973:127,131-133) found that cingular traits and supernumerary cusps contributed slightly more than expected to the total Sanghvi's G values, for each intergroup comparison. In contrast, the ridge traits (e.g. shovelling) added less than expected to the differences between study populations, but the discrepancies were generally rather small. Many of the same features were used in this analysis of Iroquoian samples (in fact, only labial ridging was not considered by Scott), and it seems likely that their contributions to the total MMD value would also be equivalent for each intersite distance calculation.

The basic equation given by Grewal-Smith (1962) for the distance between two populations is the following:

$$MMD = \frac{\overset{N}{\underset{i=1}{E}} (\theta_1^i - \theta_2^i)^2 - (1/n_1^i + 1/n_2^i)}{N},$$

where:

N = the number of traits considered in the analysis;

E = the sum of all MMD values for the N traits considered; i.e., trait$_1$, trait$_2$, trait$_3$... trait$_N$;

i = the variable representing any specific trait;

θ_1^i = the transformed incidence-fraction of trait #i in population #1;

θ_1^i = the transformed incidence-fraction of trait #i in population #2;

n_1^i = the number of observations (i.e. antimeres, teeth, individuals) in population #1 taken for trait #i;

n_2^i = the number of observations (i.e. antimeres, teeth, individuals) in population #2 taken for trait #i.

The computation of the MMD initially requires the transformation of the original incidence fractions or proportions of each trait into angular values (θ). It should be noted that transformation formulae generally require that these incidences be expressed as fractions or proportions, and not as percentages. The transformation statistic used here is the Freeman-Tukey (1950) equation, because it is the best at correcting the variance error involved with very low trait proportions, and also compensates for deviations resulting from small sample sizes (Green and Suchey, 1976; Molto, 1983:182-183).

The Freeman-Tukey (1950) transformation takes the following form:

$$\theta = 1/2 \arcsin \frac{(1-2k)}{(n-1)} + 1/2 \arcsin \frac{(1-2\ (k+1))}{(n+1)},$$

where k/n = the observed trait proportion. This transformation requires the substitution of $n_1^i + 0.5$ and $n_2^i + 0.5$ for n_1^i and n_2^i, respectively, to remove the error resulting from random sample fluctuation, so that the complete equation is the one given below:

$$\text{MMD} = \overset{N}{\underset{i=1}{E}} \frac{(\theta_1^i - \theta_2^i)^2 - (\ 1/(n_1^i + 0.5) + 1/\ (n_2^i + 0.5)\ )}{N}.$$

8.4 Results and discussion of MMD analysis.

The theta values for left and right sides were pooled for use in the MMD equation (see Tables 16a,b,c, pp. 301-303). Initially, only the values for the left side were used, but the analyses with one-side and two-side data yielded approximately the same results, and the latter is thought to give a more accurate representation of intergroup affinities (Green et al., 1979; Ossenberg, 1981). It should also be noted that because theta values cannot be calculated for frequencies of 100%, the proportions for the shovelling feature (on I^1 and I^2) were given in terms of trait absence rather than trait presence. Bartlett's adjustment was used for all dental characters with an incidence of 0 or 1 (see Sjøvold, 1973).

The results of the MMD analysis are given in Table 17, (p. 304). All intergroup differences are significant, except for the Shaver Hill-Carton comparison, which yielded a somewhat ambiguous negative value. Several other observations are evident from this table:

(1) the Shaver Hill and Carton populations are the closest groups, by a wide margin;

(2) the Shaver Hill and Carton populations (especially the former) are much closer to the Sopher group than to the Grimsby or Kleinburg samples;

TABLE 16a. DATA USED FOR CALCULATION OF MMD FOR IROQUOIAN POPULATIONS: GRIMSBY AND SHAVER HILL SITES.

Traits	Grimsby				Shaver Hill			
	Right	Left	n	Theta	Right	Left	n	Theta
Maxillary								
I1 shovel absent	0/30	0/25	55	1.427	0/12	0/15	27	1.362
I1 labial ridge	0/27	4/28	55	0.630	3/13	3/13	26	0.546
I2 shovel absent	1/33	2/36	69	1.121	1/11	1/10	21	0.886
I2 labial ridge	4/34	5/34	68	0.811	0/7	2/9	16	0.787
I2 lingual tubercle	4/38	4/41	79	0.907	2/11	3/11	22	0.550
C lingual tubercle	10/27	7/31	58	0.419	5/17	0/15	32	0.730
M1 hypocone[a]	27/54	30/54	108	-0.055	38/44	26/33	77	-0.713
M1 Carabelli trait	33/50	30/44	94	-0.344	22/42	13/32	74	0.053
M2 hypocone[a]	1/49	0/43	92	1.320	0/22	2/25	47	1.112
M2 Carabelli trait	3/49	3/45	94	1.024	0/21	3/24	45	1.013
Mandibular								
P4 extra lingual cusps	6/40	6/41	81	0.769	7/19	1/13	32	0.506
M1 + pattern	1/31	1/33	64	1.178	3/32	1/30	62	1.030
M1 protostylid[b]	2/30	2/33	63	1.035	2/33	0/26	59	1.162
M1 cusp #6	4/38	6/38	76	0.814	8/26	8/22	48	0.333
M1 cusp #7	2/32	4/32	64	0.928	8/32	6/27	59	0.543
M2 Y pattern	4/30	1/32	62	0.972	0/21	1/14	35	1.166
M2 protostylid[b]	1/30	2/33	63	1.100	1/24	2/26	50	1.042
M2 cusp #5	17/33	17/35	68	0	14/16	17/23	39	-0.613
M2 cusp #6	3/33	5/35	68	0.854	4/11	3/15	26	0.461
M2 cusp #7	1/31	0/31	62	1.266	2/22	2/24	46	0.942

NB: Bartlett's adjustment (Sjϕvold, 1973) used for all traits with an incidence of 0.

[a] Full-sized hypocone; 5-cusped molars excluded from samples.

[b] Large pits excluded from incidences.

TABLE 16b. DATA USED FOR CALCULATION OF MMD FOR IROQUOIAN POPULATIONS: CARTON AND SOPHER SITES.

	Carton				Sopher			
Traits	Right	Left	n	Theta	Right	Left	n	Theta
Maxillary								
I1 shovel absent	0/17	0/3	10	1.213	0/15	0/12	27	1.362
I1 labial ridge	3/7	0/3	10	0.374	3/15	2/13	28	0.670
I2 shovel absent	0/14	0/12	26	1.357	0/7	0/9	16	1.294
I2 labial ridge	2/12	1/11	23	0.789	3/8	2/8	16	0.362
I2 lingual tubercle	2/13	1/12	25	0.821	1/8	2/10	18	0.686
C lingual tubercle	6/29	10/32	61	0.487	5/18	2/10	28	0.504
M1 hypocone^a	59/67	45/57	124	-0.737	29/36	25/33	69	-0.591
M1 Carabelli trait	33/64	26/54	118	0	27/36	14/32	68	-0.204
M2 hypocone^a	0/38	1/27	65	1.273	1/17	2/21	38	0.964
M2 Carabelli trait	0/39	1/32	71	1.286	3/17	1/20	37	0.869
Mandibular								
P4 extra lingual cusps	4/27	6/25	52	0.648	4/14	1/18	32	0.730
M1 + pattern	4/52	5/45	97	0.938	1/18	1/33	51	1.131
M1 protostylid^b	3/57	2/51	108	1.118	1/18	5/34	52	0.856
M1 cusp #6	11/22	9/20	42	0.046	6/16	12/33	49	0.263
M1 cusp #7	15/48	8/42	90	0.505	4/18	7/34	52	0.602
M2 Y pattern	0/40	4/46	86	1.113	2/25	9/21	46	0.085
M2 protostylid^b	4/39	2/46	85	1.014	0/26	1/21	47	1.221
M2 cusp #5	26/31	32/38	69	-0.736	1/26	18/21	47	-0.702
M2 cusp #6	7/22	7/23	45	0.379	7/20	4/18	38	0.423
M2 cusp #7	2/35	1/42	77	1.145	5/25	5/21	46	0.583

NB: Bartlett's adjustment (Sjøvold, 1973) used for all traits with an incidence of 0.

[a] Full-sized hypocone; 5-cusped molars excluded from samples.

[b] Large pits excluded from incidences.

TABLE 16c. DATA USED FOR CALCULATION OF MMD FOR IROQUOIAN POPULATIONS: KLEINBURG SITE.

Traits	Kleinburg Right	Kleinburg Left	n	Theta
Maxillary				
I1 shovel absent	7/174	6/180	354	1.178
I1 labial ridge	26/212	23/251	463	0.905
I2 shovel absent	8/163	10/161	324	1.089
I2 labial ridge	3/196	11/182	378	1.057
I2 lingual tubercle	3/207	21/193	400	0.975
C lingual tubercle	11/254	9/295	549	1.182
M1 hypocone[a]	225/342	234/356	698	-0.320
M1 Carabelli trait	136/200	154/219	419	-0.393
M2 hypocone[a]	52/320	21/303	623	0.870
M2 Carabelli trait	40/240	38/209	449	0.709
Mandibular				
P4 extra lingual cusps	23/226	25/232	458	0.909
M1 + pattern	18/215	16/221	436	1.001
M1 protostylid[b]	12/157	11/171	328	1.030
M1 cusp #6	91/146	87/142	288	-0.238
M1 cusp #7	34/235	29/225	460	0.810
M2 Y pattern	13/192	28/193	385	0.903
M2 protostylid[b]	22/151	26/149	300	0.745
M2 cusp #5	174/193	184/196	389	-0.994
M2 cusp #6	58/133	67/127	260	0.038
M2 cusp #7	10/205	22/176	381	0.979

NB: Bartlett's adjustment (Sjφvold, 1973) used for all traits with an incidence of 0 or 1.

[a] Full-sized hypocone; 5-cusped molars excluded from samples.

[b] Large pits excluded from incidences.

TABLE 17. MMD AND ASSOCIATED STATISTICAL PARAMETERS - RESULTS OF ANALYSIS.

	Grimsby	Shaver Hill	Carton	Sopher	Kleinburg
Grimsby	-	1.232	1.673	2.257	3.817
Shaver Hill	.014	-	-0.409	0.893	1.607
Carton	.016	.021	-	1.105	1.756
Sopher	.015	.020	.021	-	2.312
Kleinburg	.005	.011	.012	.011	-
Grimsby	-	3.203	3.642	4.228	5.806
Shaver Hill	7	-	1.549*	2.853	3.586
Carton	4	10	-	3.063	3.731
Sopher	3	9	8	-	4.290
Kleinburg	1	6	5	2	-
Total Rank	15	32	27	22	14

The first matrix presents the MMD (above) and s (below); the second matrix presents the degree of isolation (above) and the rank order (below).

The degree of isolation (DI) is given by the formula: DI = (MMD + 2) - 2s, (after Jackes, in press). Values less than 2.0 are not significant (*).

(3) the Shaver Hill and Carton populations are distinctly closer to the Grimsby sample (especially the former) than to the Kleinburg group;

(4) the Sopher population is somewhat closer to the Grimsby sample than to the Kleinburg group;

(5) the Grimsby and Kleinburg populations are the most distantly related of any two samples;

(6) the Kleinburg population appears to be the most distinct group, while the Shaver Hill, Carton and Sopher samples cluster together.

These results are generally similar to those given by P.J. Wright (1974:203-204). His cumulative X^2 analysis indicated that the Shaver Hill and Carton (Neutral) populations were the most strongly related groups, and also that the Shaver Hill population was closer to the Sopher (Huron) sample than the Carton population. None of these site differences were found to be significant; they may have been underestimated, because Wright was forced to use adjusted X^2 values for most of the ossuary trait comparisons (due to small tooth-sample sizes), and this particular statistical technique minimizes the dissimilarity between any two populations.

K.E. Wright (1977:65-66,69-71) found a strong affinity among the Shaver Hill, Carton and Sopher samples, and a significant difference between these three samples and the Kleinburg material. This was not expected, because the

Kleinburg remains were thought to represent a Huron population by some workers, and therefore should have been demonstrably related to the Sopher group. Wright explained this discrepancy by suggesting that the Kleinburg population might actually represent a mixture of Amerindian and European (French) groups, or it might be younger than the assigned date (AD 1600), or the traits chosen for the distance analysis did not adequately reflect interdemic gene differences.

This situation was further complicated when a comparison of the four Iroquoian ossuaries with a Burlington (white) cast series indicated that the Kleinburg people were intermediate between the other three groups and the urban whites. However, conclusions drawn from this last analysis are rather dubious, as two different kinds of samples were treated as equivalent in nature. The Burlington population was comprised of families from several different European regions, and consisted of known individuals. In contrast, the ossuary remains represented demes from one area, and the dentitions could not be accurately sexed or aged, or even assigned to separate skeletons (P.J. Wright, 1974:69-70, 205-208).

A matter of some concern is the failure to find significant differences between the Sopher material and the Shaver Hill - Carton groups. K.E. Wright (1977:48-68) used both the MMD and the Sanghvi's G test for her analysis, and stated that the two techniques gave similar estimates of relative biological distance (Wright, 1977:71). It should be noted that the application of the latter formula to compare the medium-sized Kleinburg samples (n = ca. 100 - 350) to the small or very small samples from the other ossuaries (n = ca. 10 - 60) is a rather dubious statistical procedure, for the reasons outlined above (Subsection 8.3). However, the MMD evaluation should have yielded results approximating those presented here, assuming that the traits used by Wright were good discriminators for Iroquoian populations.

The dental attributes employed by K.E. Wright (1977:55-58) in her intergroup comparisons were generally the same as those used here~~,~~ except that four of her features and 10 trait-categories were not considered. Lingual tubercles on the central incisor (I^1) were found to be relatively rare and prone to differing interobserver interpretation and scoring results. For the same reasons, shovelling and labial ridging on the lower incisors (I_1 and I_2) were judged to be unsatisfactory for MMD analysis; these characters required the rating of very subtle degrees of trait presence, as only weak elevations occurred on the two teeth. Anterior transverse crests on the upper premolars (P^3 and P^4) and molars (M^1 and M^2) quite possibly have a low genetic component and their utility in biological distance estimation remains to be demonstrated. Wright also included lingual tubercle frequencies on the anterior premolar (P_3) in her evaluation, but many of these elements ~~are~~ likely to be fortuitous in nature (Scott et al., 1983).

However, both Wright's analysis and the one presented here agree that the position of the Sopher population is rather anomalous, as it is surprisingly close to the Shaver Hill and Carton groups and unexpectedly distant from the Kleinburg sample. This may be partly due to the nature of the Sopher remains; these consist mainly of loose teeth that had to be identified as correctly as possibly using morphological criteria (P.J. Wright, 1974:206-207). It should be noted that this is often a difficult exercise, especially in regard to multi-element classes (e.g. molars), and is prone to a certain degree of error, even for very experienced workers (Taylor, 1978:290-294,317-322). In fact, Korenhof (1960:326) could not make an accurate serial determination of the upper molars in his Malayan collection. It is possible, then, that mistakes in tooth-identification biased the trait proportions given by Wright for the Sopher ossuary material.

In contrast to the Sopher material, most of the teeth from the Shaver Hill and Carton sites were apparently recovered in the form of partial or complete dental arcades (P.J. Wright, 1974:69,205-206). The bulk of the material from Kleinburg that was actually analyzed also consisted of elements found in maxillary or mandibular fragments (ca.

31.4% of the entire assemblage). However, there is some question about how many of the "accurately identified" antimeres (if any) were in a dissociated condition (K.E. Wright, 1977:33). It can be assumed, though, that tooth-side and serial position were correctly determined in the vast majority of cases for the Shaver Hill, Carton and Kleinburg specimens.

The most important source of bias in biological distance estimation is that contributed by interobserver error. In the case of the Iroquoian ossuary analysis presented here, the clustering of the Shaver Hill, Carton and Sopher populations may be due to the fact that all these groups were scored by the same investigator. The variance exhibited among this group cluster, the Kleinburg sample and the Grimsby sample might therefore be the result of three sets of material being scored by three different individuals.

Unfortunately, it was not possible to conduct comparative scoring sessions with either P.J. Wright or K.E. Wright. P.J. Wright is now the regional archaeologist for southeastern Ontario and has apparently not looked at a tooth in over a decade (B.M. Newton, Archaeological Survey of Alberta, pers. comm., 29/4/1986). K.E. Wright is presently doing research in the field of immunology, and has not recently worked on dental morphology (E.J.E. Szathmary, McMaster University, pers. comm., 22/1/1987). The problem of standardization was aggravated by the fact that Dahlberg's (1956) and Turner's (1970) reference plaques were not available to any of the investigators who worked on Iroquoian dental morphology, with the exception of P#1 (used by Wright, 1977:14-15).

Nichol and Turner (1986) examined interobserver scoring variance for a number (45) of ranked and discrete tooth characters, using standard reference plaques. While rating-discordance between the two workers was rather frequent for some traits in their study sample, a statistical analysis demonstrated that these discrepancies were generally random in direction and tended to cancel out. The authors concluded that most of the dental attributes considered could be graded with "adequate" interobserver reliability. However, there were 10 exceptional trait-categories, three of which were used in the (1985) MMD estimation done for this study: lingual tubercles on the anterior teeth (viz. I^2 and C^1) and Y-groove pattern on the second molar (M_2). Disparities in scoring these variations were prone to a statistically significant degree of directional bias, although it should be noted that other investigators would likely have problems with different features.

An intergroup comparison of theta values, on a trait by trait basis, gives an approximate idea of the effects of interworker scoring variance (see Table 18, p. 311). If the MMD results simply reflect observer scoring tendencies,

TABLE 18. COMPARISON OF TRAIT THETA VALUES FOR DIFFERENT GROUPS.+

Traits	Distant Group	Medial Group	Trinal Cluster- 3 Closest Groups			Medial Group	Distant Group
MAXILLARY							
I1 shovel absent	[KL	CA]	SH*	SO*	GR*		
I1 labial ridge		CA	SH*	GR*	SO*		KL
I2 shovel absent	SH		KL*	CA*	[SO	CA]	
I2 labial ridge	SO		SH*	CA*	GR*	KL	
I2 lingual tubercle	SH	SO	CA*	GR*	KL*		
C1 lingual tubercle			GR*	CA*	SO*	SH	KL
M1 hypocone**			$\underline{\text{CA}}$*	$\underline{\text{SH}}$*	$\underline{\text{SO}}$	$\underline{\text{KL}}$	$\underline{\text{GR}}$
M1 Carabelli trait			$\underline{\text{KL}}$*	$\underline{\text{GR}}$*	$\underline{\text{SO}}$	[CA	SH]
M2 hypocone	[KL	SO]	SH	CA*	GR*		
M2 Carabelli trait		KL	SO	SH*	GR*		CA
MANDIBULAR							
P4 extra lingual cusp	SH		CA*	SO*	GR*	KL	
M1 + pattern			CA*	KL*	SH*	[SO	GR]
M1 protostylid	SO		KL*	GR*	[CA*		
M1 cusp 6**		$\underline{\text{KL}}$	CA	SO*	SH*		GR
M1 cusp 7**			CA*	SH*	SO*	KL	GR
M2 Y pattern	SO	[KL	GR]	CA*	SH*		
M2 protostylid	KL		CA*	SH*	GR*	SO	
M2 cusp 5**		$\underline{\text{KL}}$	$\underline{\text{CA}}$*	$\underline{\text{SO}}$*	$\underline{\text{SH}}$		GR
M2 cusp 6**		KL	CA*	SO*	SH*		GR
M2 cusp 7	SO		SH*	KL*	CA	GR	

NB: CA = Carton; GR = Grimsby; KL = Kleinburg; SH = Shaver Hill; SO = Sopher.
$\underline{\text{CA}}$ Negative theta value for trait.
+ Theta values given in order of increasing magnitude from left to right.
[ ] Closely related groups (within 0.100), aside from trinal cluster.
* Proximate groups within 0.100 of one another.
** Theta values may reflect interobserver scoring variance.

then the theta values of the Shaver Hill, Carton and Sopher populations should consistently cluster together, while those of the Grimsby and Kleinburg samples should generally fall in the "medial" or "distant" categories. However, Grimsby sample values occur in the "trinal cluster" class almost as often as Shaver Hill and Carton and more often than Sopher sample values, and the Grimsby values are found combined with two of the latter (Shaver Hill, Carton or Sopher) nearly twice as often as the predicted occurrence of the Shaver Hill - Carton - Sopher association. The data presented in the table also indicate that intergroup relationships are not simply a reflection of geographic proximity.

Discontinuous cranial traits have also been used in MMD comparisons of Iroquoian populations. Molto (1983:212,222) found that Carton, Garland and Kleinburg clustered together, relative to the other site samples examined; however the latter were rather widely distributed in space and time. This investigation did not consider the Grimsby, Shaver Hill and Sopher groups. Jackes' (in press) analysis of five samples indicated that significant differences occurred between any two groups, and that the Grimsby and Kleinburg populations were the most distantly related (except for the much older and geographically removed Serpent Mounds material). Data from four of these sites (including Fairty and Tabor Hill) were taken from Molto's study, but this would not explain the great disparity between the Grimsby and Kleinburg samples.

8.5 Conclusions for MMD analysis of five Iroquoian samples.

(1) The Shaver Hill and Carton populations are the two most closely related groups.

(2) The relatively great biological distance found between the Grimsby and Kleinburg populations is not an artifact of interobserver scoring variance, as a similar result was given by another study which used discontinuous cranial traits.

(3) The position of the Sopher population is ambiguous; its apparent relationship with the Shaver Hill - Carton group cluster may be the result of several factors, including gene flow with the latter and perhaps interobserver scoring error.

(4) The Kleinburg population is the most distinct group; this is indicated by MMD estimates using both dental and cranial features.

(5) An intergroup comparison of the theta values, on a trait by trait basis, demonstrates that the MMD results of the present study cannot be explained simply by interobserver scoring variance or by geographic proximity of the samples considered.

CHAPTER 9.

SUMMARY AND CONCLUSIONS.

This thesis was primarily concerned with the dental morphology of the Grimsby people. The major objective was therefore to determine the frequencies and phenotypic expressions of certain tooth characters, namely, those that have been widely used in describing human teeth and differentiating closely or distantly related groups in odontographic studies. The thesis body (Chapters 3 - 7) dealt with ~~this objective~~ by carefully presenting the methodology used and the observations recorded for the Grimsby cast sample.

Additionally, it was necessary to consider the selected features in terms of their structural and surficial anatomy, phylogenetic background, racial and geographic variation, lateral asymmetry, possible sexual dimorphism and mode of inheritance, in order to gain some idea of their suitability for the stated aim (as well as those objectives given below). A summary of some aspects of the nature of these attributes is given in Table 19 (p. 315). The traits examined were generally found to be more or less bilaterally manifested and apparently transmitted by autosomal chromosomes, and therefore of use in biological distance analyses of ossuary populations.

TABLE 19. FEATURES EXAMINED FOR GRIMSBY POPULATION.

Tooth	Dental Characters	Bilaterality	Dimorphism
I^1	Winging	1/9	Sig?
I^1;	Labial shape*	22/22;	No
I^1; I^2	Shovelling*	32/32; 35/38	No
I^1; I^2	Labial ridging	6/8; 4/7	No
I^1; I^2	Lingual tubercles	0/1; 3/6	No
I^1; I^2	Cingular Welts	1/5; 1/5	No
I^1; I^2	Medio-lingual ridges	7/10; 1/6	No
I^1; I^2	Interruption grooves	0/1; 4/8	No
I_1	Winging	8/18	Sig?
I_1; I_2	Shovelling	15/16; 21/24	Sig?
C^1	Shovelling	2/2	No
C^1	Lingual tubercles	10/11	Yes
C^1; C_1	Distal accessory ridge	9/9; 31/31	No; Yes
P_4	Extra lingual cusp	6/8	No
P_4	Groove pattern*	44/48	No
P_3; P_4	Main ridge bifurcation	2/10; 4/11	Sig?
P_3; P_4	Extra occlusal ridges	29/35; 29/32	Sig?
M^1; M^2; M^3	Hypocone expression*	56/60; 51/55; 35/41	No
M^1; M^2; M^3	Fifth cusp variation*	4/4; 6/6; 2/2	No
M^1; M^2; M^3	Carabelli complex	33/38; 3/4; 2/2	No
M^2; M^3	Paramolar tubercle	0/1; 1/2	No
M_1; M_2; M_3	Groove pattern	38/38; 32/39; 14/15	No
M_1; M_2	Deflecting wrinkle	11/11; ?/1	No
M_1; M_2; M_3	Fifth cusp	44/44; 22/22; 4/4	No
M_1; M_2; M_3	Sixth cusp	6/6; 6/7; 0/1	No
M_1; M_2	Seventh cusp	4/4; 0/1	No
M_1; M_2; M_3	Protostylid complex	2/6; 2/11; 1/7	No

NB: Underlined features are those used in MMD analysis.

* Bilaterality proportions refer to grade-expression; presence-absence asymmetry did not occur.

The other two objectives involved the use of the "most diagnostic" or "most reliable" features in the biological distance analysis of five skeletal Iroquoian groups from southern Ontario (including the Grimsby sample), and the utility of these attributes for this type of comparison (see Table 19, p. 315). The distance formula applied was the Grewal-Smith Mean Measure of Divergence, which was considered to be the best statistical function for the required purpose. There was also a discussion of the practical problems (e.g. interobserver scoring variance) and theoretical difficulties (e.g. developmental "spheres of influence") involved in employing the selected dental characters in distance studies (Chapter 8).

An attempt was made to measure the influence of interworker error on the MMD results, by examination of the trait theta figures for different groups. This analysis revealed that some theta values reflected interobserver scoring variance more than others, viz. those for hypocone manifestation (M^1), and expression of the fifth cusp (M_2), sixth cusp (M_1 and M_2) and seventh cusp (M_1). Other feature values suggested the expected pattern, according to geographic proximity and presumed cultural affiliation, viz. those for labial ridging (I^2), hypocone manifestation (M^2), the Y-groove configuration (M_2), the protostylid complex (M_2), and (possibly) seventh cusp expression (M_2). However, the overall intergroup distance estimations could not be solely the result of either interobserver error, or of ethnogeographic factors, but was probably affected by both factors. Independent cranial study confirmed the relative isolation of the Kleinburg population and the marked disparity between the Kleinburg and Grimsby samples.

One of the major problems in using dental characters for biological distance computations is evaluating the effect of developmental fields on trait independence. In the Grimsby sample, the upper anterior elements showed some evidence of the influence of fields. Marked shovelling decreased considerably from the first incisor (81.3%) to the second (37.5%) to the canine (12.0%), while lingual tuberculation manifested the opposite trend, increasing distalwards from the central tooth (2.3% on I^1; 13.0% on I^2; 30.6% on C^1). However, in the case of both traits, there was a notable difference in variant frequency between the two incisors, and also between the last incisor and canine. The lower anterior dentition did not clearly exhibit similar incidence gradients; e.g. shovelling proportions rose from the first incisor (45.7%) to the second (57.1%), but distinct ridging expressions declined from the latter to the canine.

In regard to the upper cheek dentition, hypocone size greatly diminished from the anterior molar to the posterior one, with the proportion of the full-sized form (class 4) declining from 58.3% (M^1) to 10.9% (M^2) to 2.4% (M^3). The fifth cusp character did not manifest a similar trend (7.8% on M^1; 13.0% on M^2; 5.1% on M^3). However, the Carabelli polymorphism showed a decreasing incidence and degree of expression from the first molar (69.1%) to the second (7.5%) to the last (5.1%). There was a marked difference in variant frequency between the two anterior teeth (M^1 and M^2) for both hypocone reduction and the Carabelli trait.

Some evidence of "spheres of influence" was also found for the lower cheek dentition. The Y-groove configuration decreased abruptly from the first molar (89.5%) to the second (5.1%) to the last (0.0%); in contrast, the X-groove configuration rose sharply distalward (7.9% on M_1; 56.4% on M_2; 100% on M_3). While the fifth cusp does not manifest a unidirectional trend in frequency of occurrence in most populations, it did show such a gradient in the Grimsby sample, declining from the anterior molar to the posterior one when only regular crown forms were considered (100% on M_1; 52.4% on M_2; 26.7% on M_3). The seventh cusp exhibited the same tendency (10.0% on M_1; 2.6% on M_2; 0.0% on M_3). The protostylid complex displayed the opposite incidence pattern (15.8% on M_1; 26.8% on M_2; 28.0% on M_3). However, the sixth cusp was most commonly observed on the second molar (16.7%), and less often on the other two teeth (13.6% on M_1 and 6.7% on M_3). The effects of the posterior developmental fields are therefore complex and rather inconsistent.

Considering both the trait-theta analysis and potential morphogenetic field effects, the best dental attributes for use in biological distance comparisons are: the labial-ridging character (I^2), hypocone manifestation (M^2), Y-groove configuration (M_2), the protostylid complex (M_2) and seventh-cusp expression (M_2). It should be noted that evaluation of the labial-ridging character (on both I^1 and I^2) suffers from a certain degree of intraobserver error, and the character should therefore be excluded from the list on this basis. Other features which do not seem to be influenced by directional scoring bias among different workers, and are therefore of some utility in population comparisons, are: the shovel-shape variation (I^1, I^2), lingual tubercle development (I^2, C^1), Carabelli polymorphism (M^1, M^2), lingual-cusp manifestation (P_1), +-groove pattern (M_1), protostylid polymorphism (M_1) and seventh-cusp expression (M_2).

According to the MMD calculations, the Grimsby and Kleinburg populations were the farthest apart, while the Shaver Hill, Carton and Sopher samples clustered together. This result suggests that a rather unusual pattern of gene flow might have occurred, between the Neutral people of the Shaver Hill and Carton sites and the Hurons of Sopher village. In contrast, the Grimsby and Kleinburg groups seemingly had relatively limited contract. However, these interpretations can be viewed only as feasible approximations, because of the potentially significant effect of interobserver error.

Little is known about the prehistoric and historic relationships of the Neutral Iroquois with the aboriginal groups of adjacent regions. There was an economic relationship with the Petun and Huron to the north, and some evidence of close social and kinship ties between the Neutrals and the Petun (Noble, 1978). The Neutral villages most likely to be closely involved with the Petun and Huron, either in intermarriage or intrading associations, were those lying in northern Neutralia and belonging to the Annochiaronon (e.g. Carlton) and Otontarounon (e.g. Shaver Hill). Local populations of these two tribes might therefore have had some genetic interchange with Huron demes, which would account for the seemingly close relationship of the Carton and Shaver Hill samples with the Sopher group.

The Sopher remains presumably represent individuals of the Arendaronnon or "Rock Tribe" (Noble, 1971), which entered eastern Huronia ca. 1590-1600. There is some evidence that this tribe originally occupied the Kawartha Lakes region of central Ontario, but moved west in response to the attacks of the Onondaga Iroquois (Heidenreich, 1971:25,86-87). If the Sopher ossuary does in fact represent a Rock tribe population, then it is likely to date to the 1600-1610 span, rather than to the 1580-1610 period originally suggested by

Noble (1971). This would make the Sopher sample contemporary with the Shaver Hill group (dated ca. 1600-1620), but older than the Grimsby group (dated ca. 1620-1650).

The Kleinburg skeletal population remains something of a mystery. According to the MMD analysis done for this thesis, it is significantly different from both Grimsby and the Shaver Hill-Carton-Sopher cluster. Kleinburg lies somewhat outside historic Neutralia (White, 1972; Noble, 1978) and has been considered a Huron population. However, it is likely that Huron villages established on the north shore of Lake Ontario were abandoned by early contact times, probably before 1600 (Heidenreich, 1971:87-88, Maps 17,19,22). Kleinburg ossurary may therefore be older than its presumed date of ca. 1600±15. If so, it might represent a more homogenous population than Grimsby and other "late" Neutral villages, some of which are known to have incorporated refugees from other destroyed Iroquoian nations, e.g. the Wenro (Noble, 1978). This might partially explain the relatively great biological distance between the Grimsby and Kleinburg samples.

The Grimsby people are more likely to have had close contact with Neutral allies and trading partners to the south than with more northern groups like the Huron and Retun. There might also have been some degree of gene from exchange with certain Algonquin tribes in southeastern

Michigan, viz. the Mascoutins ("Fire Nation"). The Neutral cantons -- particularly those of southern Neutralia -- were in a state of perpetual warfare with the Fire Nation, and on some occasions are known to have taken several hundred prisoners in a single raid on the latter tribe (Noble, 1978). Many of these individuals were tortured and killed, but if the rest were adopted and incorporated into the tribe, which was the custom among the Five Nations (Hunt, 1940:97-98), then this would explain to some extent the differences found between the Grimsby sample and the Shaver Hill and Carton samples.

The results of the MMD analysis of five Iroquoian populations suggests the possibility that significant gene flow might have occurred between the Neutral samples at Shaver Hill and Carton, and Huron groups related to the Sopher population. The analysis is also important in that an associated trait-theta examination indicated that certain features are much less affected by intraobserver error than others, and therefore much more useful in interdemic comparisons. Finally, the thesis presents a careful and detailed study of the dental morphology of the Grimsby Neutral Iroquois.

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APPENDIX 1a. DENTAL METRICS OF GRIMSBY SAMPLE: MAXIMUM BUCCOLINGUAL MEASUREMENTS FOR MALES.

TOOTH	MEAN	STANDARD DEVIATION	NUMBER*	INDIVIDUALS
MAX RM3	10.87	0.71	48	6
MAX RM2	11.71	0.52	84	14
MAX RM1	11.80	0.35	78	13
MAX RP2	9.66	0.42	84	14
MAX RP1	9.70	0.49	84	14
MAX LP1	9.65	0.58	90	15
MAX LP2	9.51	0.44	90	15
MAX LM1	11.88	0.40	96	16
MAX LM2	11.76	0.58	84	14
MAX LM3	10.56	0.65	84	8
MND RM3	10.34	0.69	48	8
MND RM2	10.48	0.55	84	9
MND RM1	11.20	0.42	42	7
MND RP2	8.25	0.42	42	7
MND RP1	7.81	0.59	84	14
MND LP1	7.99	0.64	90	15
MND LP2	8.42	0.40	90	15
MND LM1	10.96	0.43	54	9
MND LM2	10.77	0.64	48	8
MND LM3	10.22	1.01	48	8

* Number = number of measurements (6 per individual).

APPENDIX 1b. DENTAL METRICS OF GRIMSBY SAMPLE: MAXIMUM BUCCOLINGUAL MEASUREMENTS FOR FEMALES.

TOOTH	MEAN	STANDARD DEVIATION	NUMBER*	INDIVIDUALS
MAX RM3	10.46	0.85	36	6
MAX RM2	11.53	0.63	66	11
MAX RM1	11.65	0.48	48	8
MAX RP2	9.24	0.85	66	11
MAX RP1	9.81	0.44	72	12
MAX LP1	9.72	0.50	66	11
MAX LP2	9.45	0.53	66	11
MAX LM1	11.65	0.50	54	9
MAX LM2	11.48	0.49	48	8
MAX LM3	10.75	0.53	48	8
MND RM3	10.36	0.46	36	6
MND RM2	10.63	0.29	30	5
MND RM1	11.12	0.32	42	7
MND RP2	8.24	0.45	60	10
MND RP1	7.85	0.49	48	8
MND LP1	7.96	0.39	42	7
MND LP2	8.23	0.35	48	8
MND LM1	10.98	0.32	42	7
MND LM2	10.72	0.38	48	8
MND LM3	10.33	0.19	30	5

* Number = number of measurements (6 per individual).